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Conservation status of the endangered chimpanzee (*Pan troglodytes verus*) in Lagoas de Cufada Natural Park (Republic of Guinea-Bissau)

Joana Isabel Silva Carvalho

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Tese orientada pelo Professor Doutor Luis Vicente e Doutor Tiago A. Marques, especialmente elaborada para a obtenção de grau de doutor em Biologia (Especialidade em Ecologia)

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NOTA PRÉVIA

A presente tese apresenta resultados de trabalhos já publicados ou submetidos para publicação (capítulos 2 a 4), de acordo com o Regulamento de Estudos Pós-Graduados da Universidade de Lisboa, publicado no Despacho Nº 4624/2012 do Diário da República II série nº 65 de 30 de Março de 2012. Tendo os trabalhos sido realizados em colaboração, a candidata esclarece que liderou e participou integralmente na concepção dos trabalhos, obtenção dos dados, análise e discussão dos resultados, bem como na redacção dos manuscritos.

Lisboa, 25 de Julho de 2014

Joana Isabel Silva Carvalho

Ao Christoph

Aos meus pais e avó

"As I was looking at that queer bird I spied a monkey, two monkeys, three monkeys, four, five, six, ten monkeys… were called oshengui by the natives. Then I saw more of the queer birds, and lo! I perceived they were all playing with these little monkeys—yes, playing with these oshenguis. …They followed those little monkeys as they leaped from branch to branch; sometimes I thought they would rest on the backs of the monkeys, but no, they would perch close to them, and then the monkey and the bird would look at each other. ... The oshengui would look at them and utter a kind of kee, kee, kee, and then they would move on, and the birds would follow. Day after day I would meet those birds, and then I would look for the monkeys, and was sure to see them. ... I wondered why they followed them; I could not imagine the reason. I never saw them resting on the birds, but I noticed that these birds were fond of the fruits and berries the oshneguis feed upon. … Did the birds follow the monkeys, or the monkeys the birds? I came to the conclusion that the birds followed the monkeys, whom they could hear telling them, as it were, where they could get food without searching for it."

Paul du Chaillu - Lost in the Jungle

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Contents

Abstract

In the last decades, primate populations have suffered great demographic declines due to several anthropogenic causes, and an immediate reclassification of chimpanzees to a status of ‘‘critically endangered’’ has been recommended. The western chimpanzee, *Pan troglodytes verus*, has been classified as “endangered” on the IUCN Red List since 1988, and information on the population status and ecology of the subspecies for Guinea-Bissau is scant. This dissertation aimed to assess population density and size, habitat use, nesting and feeding patterns of chimpanzee populations at Lagoas de Cufada Natural Park (LCNP), Guinea-Bissau, a forest-savannah mosaic widely disturbed by humans. Chimpanzee nests were found distant from proxies of human disturbance such as settlements and roads, pointing towards a perhaps not surprising negative influence of human disturbance on chimpanzee distribution. By comparison with previous studies for Guinea-Bissau, chimpanzee density estimates for LCNP were the lowest, and although being the least available habitat type, density estimates were highest for dense-canopy forest, the preferred habitat for nesting. Vegetation characteristics of dense forest – lower species diversity and greater availability of smaller-sized trees compared to open forest and savannah-woodland – were important predictors of chimpanzee nest abundance. Chimpanzees were selective in their choice of nest tree species, in line with other great ape studies, but in contrast with other western chimpanzee populations did not show a preference for nesting in oil-palms. Exclusive arboreal nesting observed at LCNP may be a consequence of widespread human disturbance, but better quantitative data are needed to establish to what extent the construction of elevated nests is indeed a response to predators that can climb trees. LCNP chimpanzees were selective frugivores, and diet diversity was inversely related to ripe fruit availability. Diet composition varied over the course of the dry season and among habitat types, although chimpanzees largely fed on the same plant species over the entire study area, suggesting that despite living in a highly human-modified landscape their proximity to humans does not limit their access to their preferred food resources. Given the importance of LCNP at the westernmost margin of chimpanzee geographic distribution, these findings can improve conservation decisions for the management of *P. t. verus* as well as its remaining suitable habitats.

Key-words: feeding ecology, Guinea-Bissau, human disturbance, line transect distance sampling, nesting patterns, population density, western chimpanzee.

Resumo

Os chimpanzés encontram-se classificados com o estatuto de "ameaçado" desde 1996, segundo a IUCN Red List, mas uma reclassificação desta espécie para o estatuto de "criticamente ameaçado" tem sido recomendada (p.e. Walsh et al. 2003, *Nature*). Nas últimas décadas temos assistido a um decréscimo do efectivo populacional dos chimpanzés, e várias actividades humanas e/ou doenças infecciosas têm sido apontadas como as principais causas desse declínio. Apesar de alguns estudos terem avaliado o impacto da caça ilegal, comercialização, desflorestação, actividades agrícolas de larga escala, aumento da densidade populacional humana, entre outros, em populações de chimpanzés, pouco se sabe como se traduzem quantitativamente no tamanho populacional desta espécie.

Das quatro subespécies de chimpanzé, *Pan troglodytes verus* é a segunda subespécie mais ameaçada, apresentando uma distribuição vasta mas descontínua em nove países da África Ocidental, sendo considerada rara ou perto da extinção no Burkina Faso, Gana, Guiné-Bissau e Senegal. Apesar da Guiné-Bissau constituir um importante refúgio no limite Ocidental de distribuição geográfica de *P. t. verus*, informação sobre o tamanho e densidade populacional e distribuição desta subespécie é ainda escassa. No entanto, estes dados são fundamentais para assegurar a longo prazo a sua conservação.

Deste modo, a presente dissertação tem como principal objectivo avaliar a densidade e tamanho populacional, uso de habitat, e a diversidade e composição da dieta de chimpanzés, de modo a contribuir em avaliações futuras do estatuto de conservação do *P. t. verus*. Em particular, populações do Parque Natural das Lagoas de Cufada (PNLC, Guiné-Bissau) foram escolhidas, pois além da sua ecologia ser pouco conhecida, estão distribuídas numa paisagem de fragmentos florestais intercalados com comunidades humanas. Adicionalmente, estas populações foram sujeitas em 2008 à redução de mais de 50% de floresta primária, ilegalmente desvastada para a construção de um porto de navios e abertura de uma extensa estrada.

Estimativas robustas da densidade e tamanho populacional dos chimpanzés do PNLC são apresentadas no capítulo 2 usando a abordagem de amostragem por distâncias. Devido ao facto dos chimpanzés não estarem habituados à presença humana, e como tal muito elusivos, considerou-se como sua evidência indirecta a presença de ninhos. Assim, uma contagem

individual de ninhos foi realizada durante a estação seca de 2010 e 2011, ao longo de 11 transectos lineares sistematicamente distribuídos. Comparando com outras populações da Guiné-Bissau, as densidades estimadas sugerem que nesta área protegida encontra-se a menor densidade de chimpanzés, e que a estimativa mais elevada pertence ao habitat menos disponível, i.e. florestas de canópia densa. Isto revela que os chimpanzés do PNLC constroem preferencialmente ninhos em florestas com maior cobertura de canópia.

Alguns estudos investigaram a distribuição de chimpanzés relativamente a diferentes níveis de perturbação humana, porém poucos foram os que quantificaram estas relações, particularmente a uma escala geográfica local. Neste mesmo capítulo consideraram-se as distâncias geográficas entre os ninhos e *proxies* de presença humana, tais como vilas, estradas e rios, para avaliar padrões de ocorrência de chimpanzés em relação a estas covariáveis de perturbação humana à escala da paisagem. Apesar da longa coexistência com humanos, os chimpanzés do PNLC constroem os seus ninhos longe de vilas, estradas e rios, coincidindo com a distribuição de fragmentos de floresta de canópia densa, apontando para uma não surpreendente influência negativa da presença humana na distribuição desta subespécie.

No capítulo 3 são investigados os determinantes ecológicos relacionados com a distribuição do *P. t. verus* quer à escala do habitat quer à escala da espécie de árvore utilizada para a construção de ninhos. Para tal, avaliou-se o efeito de características da vegetação – riqueza, diversidade e composição florística, densidade e área basal das árvores – na abundância de ninhos. Também se explorou o padrão de distribuição da altura de construção dos ninhos para determinar suporte para a estratégia de anti-predação. Por último, o padrão de selecção de espécies de árvores para a construção de ninhos foi investigado. A mesma contagem individual de ninhos do capítulo 2 foi usada, adicionando a cada ninho informação sobre o tipo de habitat, a espécie de árvore e a altura de construção. Diferentes tipos de habitats foram descritos ao longo dos transectos lineares (plantas com diâmetro à altura do peito > 10 cm; 2,5 m para cada lado). Com base num modelo binomial negativo inflacionado em zero (ZANB) com efeito aleatório, a abundância de ninhos mostrou estar negativamente relacionada com a diversidade florística e área basal das árvores, reflectindo preferência pela floresta de canópia densa, tal habitat caracterizado por uma baixa diversidade florística e uma elevada disponibilidade de árvores baixas. Esta preferência foi também realçada na associação positiva obtida entre a abundância de ninhos construídos apenas em espécies utilizadas na dieta e a disponibilidade de árvores baixas. O efeito positivo da riqueza e

composição florística na abundância de ninhos revela que quer a floresta de canópia esparsa quer a savana arborizada têm também um papel importante na construção de ninhos. A construção exclusiva de ninhos arbóreos sugere ser uma adaptação à presença humana, contudo, dados futuros são necessários para averiguar se a elevada altura a que os ninhos são encontrados é de facto uma resposta à presença de predadores não humanos (p.e. leopardos). Os chimpanzés seleccionam preferencialmente espécies de árvores para a construção de ninhos, e apesar da preferência pela palmeira-de-óleo (*Elaeis guineensis*) ser um comportamento observado na maioria das populações de *P. t. verus* distribuídas em mosaicos de floresta-savana, no caso do PNLC foi a segunda espécie mais utilizada, apresentando porém uma proporção de uso bastante baixa.

Entre outros, a disponibilidade alimentar determina a distribuição espacial e temporal dos chimpanzés. Com uma dieta especializada em frutos maduros dependentes da sazonalidade e padrões de selectividade na escolha de certas plantas desproporcionalmente à sua disponibilidade, os chimpanzés têm demonstrado uma certa plasticidade e flexibilidade dietária em paisagens dominadas por áreas agrícolas. No capítulo 4 é caracterizada a variação espaço-temporal da disponibilidade de plantas e a diversidade e composição da dieta de chimpanzés no PNLC. Um estudo fenológico foi realizado durante um ano através de uma amostragem focal de espécies de plantas, recolhendo-se amostras fecais e restos alimentares apenas durante a estação seca. Os resultados indicam que os frutos estão mais disponíveis durante a estação seca e que o seu pico da maturação ocorre antes do ínicio da estação das chuvas. A diversidade da dieta variou inversamente com a disponibilidade de frutos maduros, verificando-se também variação na composição da dieta durante a estação seca e entre tipos de habitats. No início da estação seca os chimpanzés seleccionam frutos de plantas da floresta densa, consumindo preferencialmente espécies da floresta esparsa no final da estação, nomeadamente frutos de figueiras. Desta selecção preferencial foi realçado o consumo de espécies de figueiras mesmo em períodos de não escassez de frutos. Porém, outras espécies revelaram ser bastante consumidas em períodos de escassez alimentar, incluindo espécies de plantas cultivadas. Nenhuma diferença significativa foi obtida entre a composição da dieta e a distância geográfica entre fezes, sugerindo que os chimpanzés têm acesso e consomem as mesmas plantas por todo o parque. Esta evidência foi ainda suportada pela ausência do efeito das vilas ou estradas, usadas como *proxies* da presença de áreas de cultivo, na composição da dieta dos chimpanzés.

A informação obtida para esta dissertação fornece conhecimento ecológico de base para populações de chimpanzés no seu limite Ocidental de distribuição geográfica. Consequentemente, permite elaborar estratégias de conservação a longo prazo fundamentadas em conhecimento científico e que suportam a recomendada reclassificação desta espécie para o estatuto de "criticamente ameaçado" (p.e. Walsh et al. 2003, *Nature*).

Palavras-chave: construção de ninhos, densidade populacional, dieta, disponibilidade alimentar, Guiné-Bissau, *Pan troglodytes verus*, perturbação humana.

Chapter 1

General Introduction

"Humanity is going to require a substantially
new way of thinking
if it is to survive"

- Albert Einstein, 1954

1.1 Anthropogenic disturbance and its effects on primate distribution

Tropical forest ecosystems are characterized by extraordinarily high plant species diversity (Hubbell 1979, Condit et al. 2002, Leigh et al. 2004), with the exception of some mono-dominant forests [e.g. *Gilbertiodendron* forests in the Democratic Republic of the Congo (Hart et al. 1989)]. Compared with tropical forests in the other main rainforest regions, African rainforests are, however, relatively poor in plant species (Richards 1996). For instance, members of plant families such as Palmae, Orchidaceae, and Lauraceae, as well as epiphytes and woody vines are comparatively rare (Primack and Corlett 2005).

Over the last 20 million years, recurring contractions and expansions have played an important role in determining plant species diversity of African forests (Malhi et al. 2013). Moreover, the evolution of human societies has shaped their landscapes in ways that are fundamentally different from those of their predecessors. Human activities have been changing forest diversity and composition, and some forests have been recovering from decades or centuries of human disturbance, such as Kibale Forest (Uganda) (Mitani et al. 2000). Yet, loss of floristic diversity and changes in species composition as a consequence of human land use are not exclusive of African forests (Aide et al. 2000).

In the last decades, primate populations have suffered great demographic declines (Brooks et al. 2006), as well as a pronounced reduction in area with suitable environmental conditions (Junker et al. 2012). These declines are due to several reasons, all having human activities and/or infectious disease epidemics as their core basis (Walsh et al. 2003). Poaching, pet trade, slash-and-burn agriculture, deforestation associated with logging and agricultural activities, large-scale agricultural plantations, introduction of exotic plant species and natural changes, explain the biodiversity loss and fragmentation of primate habitats worldwide (Chapman and Onderdonk 1998, Gippoliti and Dell'Omo 2003, Isabirye-Basuta 2008, Sá et al. 2012, Arcus Foundation 2014). Some of these human activities, such as poaching and illegal hunting (Oates 1996) affect primate populations directly, while others, such as deforestation and slash-and-burn agriculture (Hashimoto 1995, Devos et al. 2008), do so indirectly.

A recent meta-analysis by Junker et al. (2012) investigated the geographic distribution of suitable environmental conditions for eight taxa of African apes, revealing a great reduction in suitable habitat between the 1990s and 2000s. Based on that study, measures of human impact such as proximity to settlements make a large contribution to the loss of suitable ecological conditions for chimpanzees. The western chimpanzee (*Pan troglodytes verus*) suffered a decline of 11% in the area of suitable environmental conditions, the smallest loss compared with the other taxa considered. The same decline was reported for Cantanhez National Park (CNP, Guinea-Bissau), where a comparison of estimates of suitable chimpanzee habitat for 1986, 1994 and 2003 showed a loss of about 11% of the total study area (Torres et al. 2010).

Suitable habitats for chimpanzees are nowadays widely fragmented and mostly surrounded by agricultural and agro-forestry areas, especially where there is a higher human population density (Campbell et al. 2008a). The vulnerability of chimpanzees to habitat fragmentation is characterized by their low population densities, low reproductive rate, and necessity for large home ranges (Plumptre et al. 2010). Landscapes dominated by slash-and-burn agriculture are associated with low estimates of chimpanzee densities (Hockings 2007, Duvall 2008, Torres et al. 2010, Sousa et al. 2011). Further, it is common for human-primate conflicts to occur, such as crop-raiding in agricultural areas (Hockings et al. 2009), as well as transmission of diseases and pathogens between humans and chimpanzees (Campbell et al. 2008a, Sá 2013).

The effect of forest degradation on primate population size depends on the diet of the species considered, i.e. folivores *vs.* frugivores and generalists *vs.* specialists (Johns and Skorupa 1987), as well as the level of its intensity. Chapman et al. (2000) suggested that different levels of logging intensity in Kibale Forest (Uganda) determine its compatibility with primate conservation. Low-intensity selective logging is compatible, however, high-intensity logging, which is more typical in most logging operations throughout Africa and elsewhere, is not (Durant et al. 2011). The Kahuzi-Biega National Park and Kasese region in the Republic of Congo are examples of large-scale deforestation due to mining operations (Hall et al. 1998). Nevertheless, human exploitation of forest resources is inevitable and the implementation of selective logging practices has been a short-term alternative to large-scale deforestation. In Kalinzu Forest (Uganda), chimpanzees showed a preference for sleeping or feeding in selectively logged areas that were adjacent to unlogged areas (Hashimoto 1995). However, these preferences did not translate into higher chimpanzee densities in logged relative to

unlogged areas. Johns and Skorupa (1987) recommended that long-term historical data are required to compare data collected at sites with different levels of logging, varying tree species composition, and using different field methods. Also important is knowledge about the vegetation composition of forest before logging, because the intensity of the impact of logging on the primate community could be related with the extraction of important food tree species (Isabirye-Basuta 2008).

Logging is a catalyst for bushmeat hunting (Wilkie and Carpenter 1999, Poulsen et al. 2009, Abernethy et al. 2013) which contributes directly to the decline of ungulates, rodents and carnivores (Fa et al. 2002, Yackulic et al. 2011), as well as primates (Tutin and Fernandez 1984, Lahm et al. 1998, Blom et al. 2004), including chimpanzees (Hashimoto 1995, Devos et al. 2008). Moreover, wildlife consumption facilitates zoonoses, i.e. the transmission of diseases from animals to humans (Rich et al. 2009), or vice versa (Walsh et al. 2003, Bermejo et al. 2006). Alves et al. (2010) documented that at least 101 species of primates, belonging to 38 genera and 10 families, including chimpanzees, are used in traditional folk practices and in magic-religious rituals.

Logging activities usually lead to the opening of new roads, facilitating poaching and illegal hunting (Fa et al. 2014), and logging employers usually have a bigger salary than locals to buy bushmeat (Wilkie et al. 2000). Bushmeat is a common component of household economies and the price of this kind of meat is lower than meat from domestic animals (Wilkie and Carpenter 1999, Sá et al. 2012, Minhós et al. 2013). The expansion of road networks facilitates access of hunters to protected areas and transportation of illegal bushmeat in many tropical forests (Fa et al. 2002, 2014).

Besides human influence, natural barriers also determine primate distribution. The riverine barrier hypothesis suggests that rivers may act as a natural barrier to primate distribution (Harcourt and Wood 2012). In western and central Africa, the distribution of several forest-dwelling primates is also limited by rivers, whereby larger rivers have a greater barrier effect on species distribution than smaller rivers (Harcourt and Wood 2012). For instance, some forest primate species do not cross the Congo River, suggesting that it acts as the main barrier to their distribution (Harcourt and Wood 2012). In western Africa, a clear barrier to the movement of forest primates is the Dahomey Gap, which separates the western Upper

Guinean forest from the Congo Forest zone and many forest-dwelling taxa, including primates, are common on either side of the forest blocks (Booth 1958, Campbell et al. 2008b). The Dahomey Gap is a savannah corridor in proximity to one of the flanking rivers, the Volta, where its aridity acts as a barrier to those species that reach the Gap but do not cross it (Harcourt and Wood 2012). However, rivers can also allow for an easy transport of bushmeat (Fa et al. 2002).

1.2 Population size and distribution of the western chimpanzee

In western Africa, 844 species from a variety of taxonomic groups are in risk of extinction, of which 203 species are assessed as globally threatened (IUCN 2014). The western chimpanzee, *P. t. verus*, is classified as "endangered", a status that has not changed since the first IUCN inventory in 1988 (IUCN 2014). In the last 20 to 30 years, this subspecies showed a significant population decline (IUCN 2014), and further population decrease is expected. *Pan t. verus* is distributed across nine West African countries, but is already rare or close to extinct in Burkina Faso, Ghana, Guinea-Bissau, and Senegal (Kormos et al. 2003). These countries have biodiversity-rich forests, which are, however, among the most threatened (Kormos et al. 2003). The Guinean Forests of West Africa have been designated as one of the 35 global biodiversity hotspots (Myers et al. 2000, Mittermeier et al. 2011) and one of the two highest priority areas for primate conservation in the world (Mittermeier et al. 1999).

Total population estimates for *P. t. verus* range from 21,300 to 55,600 individuals (Kormos et al. 2003). The highest population density is reported for Taï National Park (Ivory Coast), corresponding to 2.19 nest builders per km^2 (Kouakou et al. 2009), contrasting with the lowest estimate of 0.13 nest builders per km^2 from the western extreme of the subspecies' distribution range, Niokolo Koba National Park (Senegal) (Pruetz et al. 2002).

For Guinea-Bissau, estimates of population size for *P. t. verus* vary between 600 and 1000 individuals (Gippoliti and Dell'Omo 2003). The first report about the status of this subspecies was published in 1940 (Monard 1940 in Gippoliti and Dell'Omo 1995), followed by a few recent assessments (Sousa et al. 2005, Brugiere et al. 2009, Sousa et al. 2011). Questionnaire surveys conducted in some villages in Guinea-Bissau and Guinea showed that the geographic range of chimpanzees is restricted by human distribution (Brugiere et al. 2009). Since most of

the human population is concentrated in northern Guinea-Bissau, suitable chimpanzee habitat is confined to the southern parts of the country (Torres et al. 2010), where *P. t. verus* occurs from the Corubal River to the border of the Republic of Guinea (Figure 1). Its distribution includes the regions of Quinara (where Lagoas de Cufada Natural Park, LCNP, is located), Tombali (with CNP and the Cacine Basin), and the Gabu sector (where Boé National Park, BNP, was recently created).

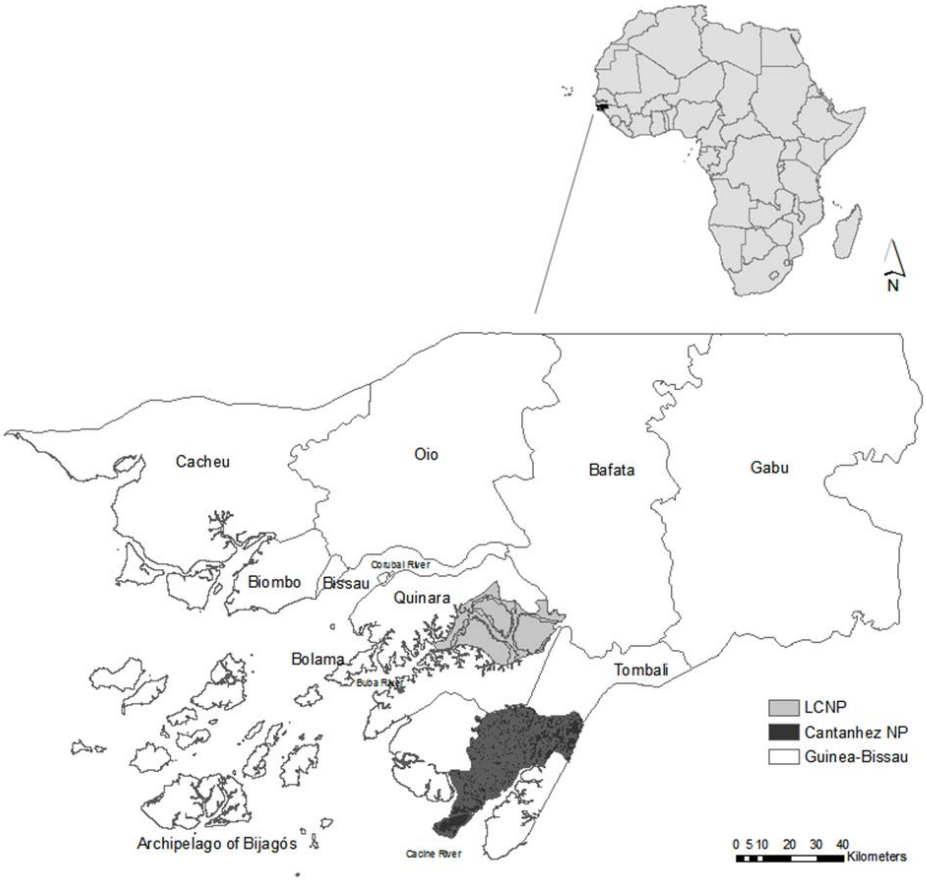

Figure 1. Localization of the Republic of Guinea-Bissau in West Africa and respective administrative regions of the country. Also, the Lagoas de Cufada Natural Park (LCNP) and Cantanhez National Park are shown.

1.3 Surveys and monitoring of primates

1.3.1 Sampling design considerations

For a robust estimate of population size and density it is important to consider suitable sampling design and methodology. *Strip transects* were used in some studies of primate density estimates (Defler and Pintor 1985, Whitesides et al. 1988). Using narrow strip transects all objects of interest can be detected, which produces an unbiased density estimator (Burnham et al. 1985, Ogutu et al. 2006). However, increasing the width of the strip transects also quickly increases the bias of the estimator.

Whenever there are animals missed in the strip transects, *Line transect distance sampling* is alternatively recommended to reduce bias through estimators that incorporate detection probability as a function of distance from the transect line (Buckland et al. 2001), and via the inclusion of additional potentially important covariates that may influence detectability (Marques and Buckland 2003). The detection function of line transects replaces the fixed sample-width of the strip transects. Another important parameter to consider is the efficiency, i.e. the ratio of the standard errors of the estimators. Due to their reduced bias and greater efficiency, line transects have become preferred over strip transects (Burnham et al. 1985, Buckland et al. 2010a).

This preference is supported by further advantages: no assumptions are required about the detection function, transect width can be increased without increasing bias, and missed objects can be accounted for in the analysis (Buckland et al. 2001). In distance sampling missed targets are accounted for by the detection function, allowing for a robust estimate of animal density (Cassey 1999). Additionally, line transects often provide greater accuracy than is normally achieved by strip transects (Buckland et al. 2001), and it is a suitable technique for estimating animal densities in dense forests (Blom et al. 2001).

Following the recommendations for an adequate study design (Buckland et al. 1993, 2001), capable of yielding robust density estimates for a wider study area, linear transects are superimposed over the study region as a grid of equally-spaced parallel lines with a random start. The underlying distance sampling assumptions required for unbiased density estimates

are: objects of interest on (or above) the line are detected with certainty and at their initial location, and the distance measured between the line and the objects of interest is accurate (Buckland et al. 2001). Distance sampling is a well-established methodology that has been widely used to estimate animal densities for a diverse range of taxa and habitats ((Buckland et al. 1993, 2001, 2010b); see also http://www.ruwpa.st-and.ac.uk/distancesamplingreferences/).

Models for the detection function and corresponding estimates of detection probability, encounter rates and animal densities are typically investigated with the software DISTANCE 6.0 (Thomas et al. 2010), following the procedures outlined in Buckland et al. (2001) for model selection and model evaluation.

1.3.2 Methods for ape surveys

There is some controversy about which is the best methodology to use for ape surveys (Hashimoto 1995, Plumptre and Reynolds 1996, Boyko and Marshall 2010). As a consequence, a variety of different methods are commonly used, making comparisons of density and abundance estimates among sites often difficult (Kouakou et al. 2009). Primate survey techniques have been developed since the late 1960s (Plumptre and Cox 2006). Originally, estimates of abundance were obtained at large geographic scales via questionnaires to local people (Sugiyama and Soumah 1988). Recently, ground and aerial surveys have often been used to monitor ape distribution (Ancrenaz et al. 2004b) by applying methods of home range estimation or nest counts (Plumptre and Reynolds 1996).

The home range method relies on direct sightings of animals within a known area to estimate their range size. Since great apes usually avoid humans and often manage to hide before being detected, this method is not reliable if robust density estimates are needed. Moreover, the low visibility in dense-canopy forest underestimates ape densities (Ghiglieri 1984, Tutin and Fernandez 1984). Alternatively, methods based on indirect signs such as nests, dung, fingertips, or vocalizations have emerged (Tutin et al. 1995).

1.3.2.1 Methods using nest count surveys

Since great apes, in contrast to all other nonhuman primates (Anderson 2000), build a nest every night for sleeping or resting during the day, nest abundance has been a useful surrogate for estimating densities and population sizes as well as for assessing their home range (Fruth and Hohmann 1996, Buij et al. 2003, Devos et al. 2008). The term "nest" is used throughout this dissertation when referring to sleeping platforms built by apes, even though they differ in terms of their function from those of other nest-building animals (see Samson and Hunt 2012).

Great ape nests might be counted either individually (Ghiglieri 1984, Hashimoto 1995, Plumptre and Reynolds 1996), in groups (Tutin and Fernandez 1984, Blom et al. 2001, Buij et al. 2002, Devos et al. 2008, Inogwabini et al. 2012), or both (Marchesi et al. 1995, Hall et al. 1998, Furuichi et al. 2001a, Morgan et al. 2006). A group of nests can be defined as all nests belonging to the same age class and found along a 20 m stretch of a transect (Tutin and Fernandez 1984). Other definitions include: all nests from the same age class found within a distance of ≤30 m from the nearest other, independent of their visibility from the transect (Furuichi et al. 2001a), or 50 m from one another (Devos et al. 2008), or simply not considering any distance between them and counting all the nests from a group, defining numbers of groups (Buckland et al. 1993). Moreover, Marchesi et al. (1995) observed nests apparently different but built on the same day and belonging to the same group, which led to ignore the life span of nests in the definition of group.

While earlier research suggested that weaned chimpanzees build only one nest per day for sleeping (Ghiglieri 1984, Tutin et al. 1995), later observations of the reuse of night nests and construction of day nests for resting (Brownlow et al. 2001) indicated that nest production rates are often >1 [e.g. 1.09 nests per day for Budongo Forest (Plumptre and Reynolds 1997) or 1.143 nests per day for Taï Forest (Kouakou et al. 2009)].

The process of nest decay results from a complex interaction of vegetation type and climatic variables, which may vary temporally and spatially (Buij et al. 2003, Kouakou et al. 2009), leading to a large variation in its estimates between different studies. For this reason, it is recommended to estimate nest decay rate for each study site, otherwise a potentially large bias may be introduced into density estimates (Tutin et al. 1995, Boyko and Marshall 2010). A

similar problem was reported for surveys using other indirect signs, for instance decay rates of dung for estimating gorilla densities (Kuehl et al. 2007) or for sound production in acoustic density estimates (Marques et al. 2013).

When a site-specific nest decay rate is available, the method *standing-crop nest counts* (SCNC) is typically used and is recommended for surveying large areas and to assess the status of great ape populations (Plumptre and Reynolds 1997, Boyko and Marshall 2010). Another commonly used nest count method, known as "direct counting of newly built nests", was proposed by Hashimoto (1995) to deal with the difficulty in estimating the life span of nests. Nowadays, this method is known as *marked nest counts* (MNC) and it gives accurate estimates of densities when sufficient time is available for repeated surveys over large sample areas. The repeated surveys also allow to assess temporal trends in population size (Plumptre and Reynolds 1996, Plumptre and Reynolds 1997).

For East African study sites, biweekly intervals have been shown to be appropriate to guarantee that no newly built nests will disappear between visits (Hashimoto 1995, Plumptre and Reynolds 1996). However, in Kalinzu Forest (Uganda) old nests were detected between biweekly surveys, but as different age classes were considered during nest monitoring, old nests were excluded and MNC was performed using only age classes corresponding to new nests (Furuichi et al. 2001a).

It is important to emphasize that several other analysis techniques have emerged to deal with the time consuming process of monitoring the decay of a large and diverse sample of nests. For example, considering a Markov Chain for the state of a nest, with an absorbing state which represents nest decay, it is possible to estimate the time a nest takes to disappear based on the observation of nests (and their corresponding state) over time (van Schaik et al. 1995, Buij et al. 2003, Kühl et al. 2008). This time-efficient procedure has proven a useful tool for the rapid assessment of orangutang densities (van Schaik et al. 1995, Buij et al. 2003).

1.4 Chimpanzee sleeping sites

1.4.1 The evolution of ape nesting behaviour

The Homo-Pan divergence occurred less than 6.3 million years ago (Chen and Li 2001, Patterson et al. 2006). Nesting or resting are considered conservative elements of an ancestral suite of behaviours found in living great apes (Wrangham 1987). As there is no evidence of nesting behaviour in modern humans, it was suggested that this behaviour may have disappeared during the evolution of Hominini in the Miocenic (Fruth and Hohmann 1996). Present-day nesting patterns in primates have been explained based on the behaviour of the last common ancestor inferred from archaeological evidence (see Sept 1998).

Evidences from the common ancestor have also been helpful in clarifying the transition from arboreal to ground nesting in early hominins (i.e. before *Homo erectus*, 1.8 million years ago) (Sept et al. 1992, Hernandez-Aguilar 2009, Koops et al. 2012b), as well as from forest to more open savannah-woodlands (Sabater Pi et al. 1997). Some cognitive, manipulative, and technological abilities may have enabled early hominins to develop strategies to be safe on the ground, including for example the development of fire for predator protection. Other cognitive abilities may have evolved through long-term memory consolidation related to a better quality of sleep when resting on the ground rather than on trees, which may have allowed early hominins to change their environment (Baldwin et al. 1981, Fruth and Hohmann 1996, Samson and Hunt 2012).

Furthermore, phylogenetic reconstructions suggested that the ancestral primate may have been nocturnal and solitary, and nests or tree holes were used to protect their young in the first days, weeks, or even months, later carrying the infant to parking places outside the shelter (Kappeler 1998). Even though nest-building behaviour may have evolved several times independently among primates, great ape nests differ in their function from those built by prosimians, mainly serving as a platform during periods of resting or sleeping and as a shelter for independent young in the latter (Kappeler 1998).

On the other hand, the current behavioural patterns of nesting and ranging of great apes could be unrepresentative of their ancestral ones due to modern land-use patterns of human foragers

(Sept 1998), and the influence of climatic changes (Isbell and Young 1996). Humans and great apes have been partners on the landscape, and their local expression of nesting patterns has been influenced by this relationship (Sept 1998, van Schaik 2002).

1.4.2 How do chimpanzees build a nest?

Nest building behaviour is generally very similar among great apes: tree branches are radially bent and broken over a foundation of stronger tree limbs, sometimes intertwining adjacent trees, and then smaller twigs are folded over the edge to form a circular frame. The main branches are then woven together and detached leafy twigs are often added to line the nest (Goodall 1962, Fruth and Hohmann 1996). The time taken to complete a nest ranges from 30 sec to 20 min (Anderson 2000). Nest structure varies depending on whether the nest is for night sleeping or day resting, day nests being structurally simpler, less solid, and constructed in feeding trees at feeding height (Goodall 1962, Plumptre and Reynolds 1997, Brownlow et al. 2001). Despite some overlap in terms of structural characteristics between both types of nests (Goodall 1962), sleeping nests are generally more solid and decay more slowly than day nests (Plumptre and Reynolds 1997).

Only weaned chimpanzees build their own nest each night while infants until two and a half years of age sleep with their mothers (Goodall 1962). Between two to six chimpanzees may sleep together in a single tree or in nearby trees, and sometimes small groups with the mother and her infant or juvenile until five years of age or feeding groups are observed (Goodall 1962).

1.4.3 The selection of sleeping site and nesting trees

Ranging patterns of animals are shaped by environmental and historical constraints as well as geographic influences (Kamilar 2009). Moreover, factors related to the behavioural ecology of the species, such as territoriality, localization of sleeping sites, predation, and competition for food or mates may play a role (Nkurunungi and Stanford 2006).

Among primates, the selection of sleeping sites has been explained by a number of non-exclusive hypotheses: anti-predation [pigtailed macaques (Albert et al. 2011), Guinea baboons (Anderson and McGrew 1984), golden backed uacaris (Barnett et al. 2012), gibbons (Cheyne et al. 2012)], thermoregulation [chimpanzees (Koops et al. 2012a), gorillas (De Vere et al. 2011)], and antipathogen [gibbons (Whitten 1982), proboscis monkeys (Feilen and Marshall 2014)]. The selection of nesting sites by Kibale chimpanzees (Uganda), for instance, was suggested to be associated with places with low abundance and diversity of anopheline mosquitoes, which seems to be an adaptation to reduce their risk in acquiring malaria infections (Krief et al. 2012).

Many primates reuse sleeping sites due to food availability [e.g. chimpanzees, (Hernandez-Aguilar 2009), gorillas (Iwata and Ando 2007), orangutans (Ancrenaz et al. 2004a), and bonobos (Hashimoto et al. 1998)]. In Ugalla (Tanzania), the reuse of sleeping sites by chimpanzees occurs also for safety reasons or for meeting other chimpanzees that had been in another party (Moore 1996, Ogawa et al. 2007). The reuse of sleeping sites can lead to the reuse of nest trees, as evidenced by the presence of nests in a different decay stage within the same tree (Goodall 1962, Brownlow et al. 2001, Hernandez-Aguilar 2006).

Chimpanzees show great selectivity regarding nest tree species as they only use a subset of the total available tree species richness for nesting (Furuichi and Hashimoto 2004, Ndimuligo 2007, Stanford and O'Malley 2008, Koops et al. 2012a). Nest tree species selection is not an exclusive behaviour of chimpanzees, although they may be more selective than other great apes (Fruth and Hohmann 1993, Hashimoto 1995, Rothman et al. 2006). Nest tree species selection has also been linked to certain physical characteristics of trees, such as diameter at breast height (dbh), tree height, and height of the lowest branch, among others (Hernandez-Aguilar 2006, Hernandez-Aguilar et al. 2013). Nonetheless, no single characteristic has been found sufficient for explaining preferences in terms of nest tree species (Hernandez-Aguilar 2006, Stanford and O'Malley 2008).

Stewart et al. (2007) pointed out two other important aspects related to the selection of nest tree species: nest building effort (i.e. force required for nest construction, nest complexity, and additional building material necessary) and the consequent comfort of the nest (assessed by physical and visible discomfort and nest softness). The authors found that the increase of

building effort by Fongoli chimpanzees (Senegal) had no significant effect on comfort of the nest as a whole, however, more complex nests were also more comfortable centrally where most of a chimpanzee's body-weight is distributed during sleeping (Stewart et al. 2007).

1.4.4 The function of arboreal nesting

Ecological and social criteria for sleeping nest site selection by chimpanzees seem to not apply in the same manner as for resting nest sites, either for ground nesting (Koops et al. 2007) or arboreal nesting (Brownlow et al. 2001). Several studies have documented that chimpanzees build nests on the ground for resting in day time or for sleeping at night (Anderson 2000, Furuichi and Hashimoto 2000, Koops et al. 2007, Hicks 2010, Koops et al. 2012b, Last and Muh 2013). Ground nesting is usually assigned to chimpanzee males, which build them below arboreal sleeping nests or, where no arboreal nests are present, close to day nests. Additionally, it was demonstrated that the occurrence of ground nesting is not influenced by seasonality, altitude, slope, nest tree species, and availability of terrestrial herbaceous vegetation, suggesting that this behaviour may be socially rather than ecologically determined (Koops et al. 2007). Nevertheless, ground nesting is very rare in wild chimpanzees, especially at night, and seems to occur where predation pressure or availability of tall trees are low (Matsuzawa and Yamakoshi 1994, Anderson 2000, Pruetz et al. 2008, Stewart et al. 2011, Koops et al. 2012a, Koops et al. 2012b, Last and Muh 2013).

On the other hand, arboreal nesting is most frequent and its function has been explained through the following non-mutually exclusive hypotheses: antipredation (Baldwin et al. 1981, McGrew 2004, Pruetz et al. 2008, Hernandez-Aguilar et al. 2013), antipathogen (Fruth and Hohmann 1996, Anderson 1998, Krief et al. 2012), thermoregulation (McGrew 2004, Koops et al. 2012a, Samson and Hunt 2012), and promotion of mental health (Fruth and Hohmann 1996, Anderson 1998). Several studies suggest that nest height as well as certain physical characteristics of trees such as tree height and canopy cover, among other variables, are important determinants of arboreal nesting patterns. These variables are important to assess evidence for or against the predation avoidance hypothesis, i.e. that elevated nest height is a predator defense strategy (Goodall 1962, Baldwin et al. 1981, Pruetz et al. 2008).

Other advantages associated with arboreal nesting are: nesting in trees guarantees easier communication among group members (Plumptre and Reynolds 1997, Brownlow et al. 2001, Furuichi and Hashimoto 2004, Sousa et al. 2011, Burnham et al. 2013); nests are built leaving an "escape route", as a nest may be left without having to descend to the ground immediately below the nest tree (Anderson et al. 1983); when only small trees are available nests are built at the tree top (Goodall 1962, Hernandez-Aguilar 2006); and chimpanzee males build nests lower than females either as a way to protect them from predators or because their greater weight restricts them to use more resistant branches, minimizing their risk of injury from falling (Plumptre and Reynolds 1997, Brownlow et al. 2001).

1.4.5 Ecological determinants of chimpanzee nesting

Habitats with a dense canopy are commonly selected by chimpanzees, especially for nesting (Baldwin et al. 1981, Anderson et al. 1983, Brownlow et al. 2001, Basabose and Yamagiwa 2002, Sousa et al. 2011, Koops et al. 2012a). In contrast, at the chimpanzee's easternmost limit of distribution in Issa (Tanzania), despite no evident preference for forest or woodland, chimpanzees build most nests in woodland (Hernandez-Aguilar 2009).

Topographical features and vegetation attributes are ecological determinants of ape distribution (Furuichi and Hashimoto 2004, Rothman et al. 2006, Ndimuligo 2007, Feilen and Marshall 2014), including nesting patterns of chimpanzees (Goodall 1962, Baldwin et al. 1981, Goodall 1986, Sept et al. 1992, Stanford and O'Malley 2008, Krief et al. 2012). The Kibale chimpanzees (Uganda) build nests at higher altitudes where the abundance and diversity of anopheline mosquitoes is lowest, rather than in sites where they feed, suggesting this behaviour may be related to the reduction of acquiring malaria infection (Krief et al. 2012). The Bwindi gorillas (Uganda) build ground nests in open-canopy forests due to the influence of the large altitudinal and climatic differences found within the park on distribution and availability of plant species (Nkurunungi et al. 2004, Rothman et al. 2006).

Vegetation characteristics such as floristic diversity and composition, as well as forest structural attributes such as tree size and density, are commonly used in studies assessing correlates of primate abundance (Medley 1993, Furuichi and Hashimoto 2004, Wieczkowski 2004, Rovero and Struhsaker 2007, Linder and Lawler 2012, Feilen and Marshall 2014).

Studies have reported a positive effect of floristic richness and tree size, on the abundance of atelid (Cristóbal-Azkarate et al. 2005, Stevenson 2011) and cercopithecid monkeys (Rovero and Struhsaker 2007, Linder and Lawler 2012). Changes in floristic composition can be associated with changes in primate abundance (Stevenson 2011). In Kalinzu Forest (Uganda), chimpanzee nest abundance was negatively correlated with tree density and positively with fruit abundance, and was influenced by vegetation type (Furuichi and Hashimoto 2004). Vegetation correlates of primate abundance may also reflect the distribution and characteristics of those tree species preferentially selected for nesting and feeding (Furuichi and Hashimoto 2004, Ogawa et al. 2007).

1.5 Chimpanzee diet and food availability

1.5.1 Primate diets and ecology

The evolution of primate social systems was profoundly shaped by their dietary niche (Wrangham 1987), i.e. whether species are folivores, frugivores or insectivores. Certain anatomical adaptations, for instance regarding body weight and brain size, are found across primate species with similar diets (Milton and May 1976, Milton 1993). Neotropical primates with an intermediate body mass are preferentially frugivores (Hawes and Peres 2013). In general, a positive association between body weight and home range of primates is found, with folivores having smaller home ranges for their body weight than frugivores (Milton and May 1976). This is also determined by the distribution and availability of leaves and fruits: folivorous primates have a great availability of leaves in smaller areas than frugivorous primates that often depend on clumped, unstable food sources**,** as a consequence of great dispersion of fruiting trees in time and space.

Primates represent a large part of frugivore biomass (Eisenberg and Thorington 1973). It is commonly assumed that primate biomass is correlated with fruit abundance and fruit tree density, which highlights the importance of fruit availability in maintaining frugivorous primate populations (Stevenson 2001). Frugivorous primates, for instance, have a larger brain with higher intellectual capacities in terms of memory and spatial mapping of food resources than folivorous primates (Milton 1981), particularly documented in chimpanzees (Normand et

al. 2009, Janmaat et al. 2013). The larger brains in apes followed by the challenge of looking for keystone food resources and dispersed fruit foods may have acted as a selective pressure in the evolution of intelligence (Tutin et al. 1991). Moreover, regular scarcity of preferred food fostered the development of innovative and inventive behaviours, such as tool use in chimpanzees (Nishida and Hiraiwa 1982).

Other anatomical adaptations to a particular diet, such as craniodental anatomy and gut morphology, are found both in chimpanzees and gorillas, suggesting an overlap in their diets whenever they share the same range. However, the large consumption of fibrous foods by gorillas seems to be a consequence of their greater body size (Tutin et al. 1991).

The co-occurrence of *Homo*, *Pan* and *Gorilla* at Lopé Reserve (Gabon) has been influenced by their competition for sleeping sites, plant foods and animal foods (Tutin and Oslisly 1995). Over time, less competition for sleeping sites and animal foods may have occurred as *Homo* preferred open savannah sites and vertebrate prey. On the other hand, although mediated by seasonality, competition for plant foods has been more pronounced due to the high dietary overlap between *Homo*, *Pan* and *Gorilla* (Tutin and Oslisly 1995).

1.5.2 Chimpanzee diet and food availability

Many studies have shown that patterns of primate distribution and density, as well as home range, can give important insights about the availability and distribution of food resources (Chapman et al. 1995, Chapman and Chapman 1999, Balcomb et al. 2000, Stevenson 2001, Nkurunungi and Stanford 2006). As ripe-fruit specialists, the diet of chimpanzees is generally dominated by ripe fruits of high nutritional quality (Goodall 1986, Furuichi et al. 2001b), as shown by the large proportion of fruits eaten or extended feeding time dedicated to fruit consumption (Wrangham 1977, Wrangham et al. 1998). Therefore, a great quantity of seeds is typically dispersed through defecation or spitting out far away from parent trees, highlighting their important role in ecosystem functioning as both seed consumers and seed dispersers (Wrangham et al. 1994, Chapman and Onderdonk 1998).

Chimpanzees also consume other plant items such as foliage, flowers, bark, piths, among others, as well as animal items, such as mammals, birds, insects, reptiles, among others

(Anderson et al. 1983, Nishida and Shigeo 1983, Tutin et al. 1997, Hicks 2010). Tool use has played an important role in broadening chimpanzee diet (Anderson et al. 1983, Boesch and Boesch 1983, Yamakoshi 1998, Humle and Matsuzawa 2004, Hicks 2010).

Although many dietary check lists are available either from sites where chimpanzees are semi-habituated or habituated to human presence [Bossou, Guinea (Hockings 2007); Goualougo Triangle, Congo (Morgan et al. 2006); Kahuzi, DR of Congo (Basabose 2002); Ngogo, Uganda (Watts et al. 2012a); Nyungwe National Park, Rwanda (Gross-Camp et al. 2009)] or not habituated [Tanzanian sites: Kasakati (Suzuki 1969), Issa (Hernandez-Aguilar 2006), Ugalla (Moyer et al. 2006)], we are still far from a comprehensive understanding of chimpanzee diet across the species' range.

Western chimpanzees have been living in areas widely subjected to human disturbance (Kormos et al. 2003), and evidences of ecological and behavioural adaptation to habitat fragmentation and loss has been reported for some anthropogenic habitats (Hockings et al. 2009, Sousa et al. 2011). For instance, new feeding opportunities for chimpanzees arise from cultivars, and the consumption of such cultivar foods may be particularly important during periods of wild fruit scarcity (Hockings et al. 2009, Hockings and McLennan 2012, McLennan 2013).

Food availability for primates is typically assessed based on plant phenological patterns, i.e. the biological activity of plants over the course of an annual cycle related to seasonality (Hernandez-Aguilar 2006). Long-term phenological studies related to chimpanzee diet exist for forest-dwelling chimpanzees (Ghiglieri 1984, Chapman et al. 1999, Newton-Fisher et al. 2000), and for savannah chimpanzees (Hernandez-Aguilar 2006). Fruit availability varies among plant species, seasons and study sites: at some sites ripe fruits are highly abundant during the wet season (Suzuki 1969, Tutin et al. 1997, Basabose 2005, Moscovice et al. 2007, Hernandez-Aguilar 2009), whereas at other sites fruit abundance peaks during the dry season (Hockings et al. 2009), or there is a bimodal pattern with peaks in both seasons (Watts et al. 2012b). Chimpanzee ranging patterns are influenced by seasonal changes in food availability (Plumptre and Reynolds 1994, Yamakoshi 1998, Furuichi et al. 2001, Basabose and Yamagiwa 2002) and in periods of habitat-wide fruit scarcity chimpanzees exhibit a range of behavioural modifications. Their fission-fusion social organization seems to allow

chimpanzees to rapidly adapt to seasonal variation in the availability of their preferred food items (Wrangham 1979). Social adjustments commonly observed during periods of fruit scarcity include the separation into feeding or nesting parties (Chapman et al. 1995, Furuichi et al. 2001a) and/or changes in habitat use by traveling farther to find food (Basabose 2005), leading to increases in home range sizes (Hernandez-Aguilar 2009).

Another adaptation observed in chimpanzees during periods of habitat-wide fruit scarcity is the increase of consumption of fallback foods (FBFs), i.e. lower-quality food resources not usually consumed in the presence of preferred items (Wrangham et al. 1998, Furuichi et al. 2001b). Foliage, flower, bark, piths, honey, mushrooms, insects and arthropods are examples of FBFs (McGrew et al. 1988, Wrangham et al. 1998, Basabose 2002, Watts et al. 2012a). Some controversy exists concerning the best definition for FBFs (Lambert 2007, Marshall and Wrangham 2007), although there is consensus that the same class of foods may have different functions, depending on which primate species is using them (Tutin et al. 1997, Marshall et al. 2009). Fig fruits have been listed in chimpanzee diets as FBFs during periods of food scarcity (Nishida and Shigeo 1983, Tutin and Fernandez 1993, Lambert and Garber 1998, Bertolani and Pruetz 2011), as also documented for other apes such as gibbons (Marshall and Leighton 2006), orang-utans (Wich et al. 2004), and gorillas (Rogers et al. 1990). In contrast, other chimpanzee populations select *Ficus* spp. more often than expected by chance, which suggests that figs are not exclusively a FBF for chimpanzees (Tutin et al. 1997, Moscovice et al. 2007, Hernandez-Aguilar 2009, Chancellor et al. 2012).

1.6 Study site

1.6.1 Republic of Guinea-Bissau

Guinea-Bissau is a small western African country (36,125 km^2), located between the latitude 10º55’ and 12º40’N and longitude 13º38’and 16º43´W (Figure 1-2). The country’s biological resources are managed by *Instituto da Biodiversidade e das Áreas Protegidas* (IBAP, http://www.ibap-gb.org/index.html), the governmental institution responsible for the management of the protected areas (Figure 2). The principal causes underlying the increasing

degradation of Guinean-Bissau's natural resources are commercial logging, bushmeat hunting, monocultures of cashew, and human population increase (IBAP 2007).

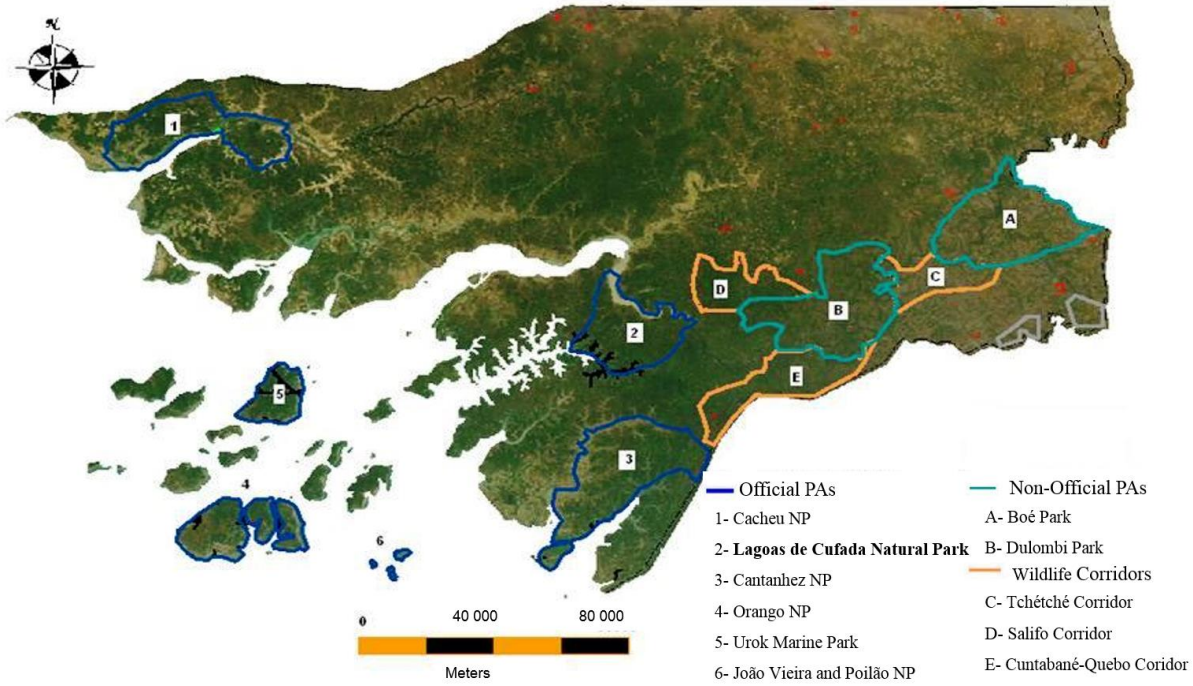

Figure 2. Location of the protected areas in Guinea-Bissau (Adapted from: http://www.thegef.org/gef/). PAs- Protected areas; NP- National Park.

Guinea-Bissau is located in the Guinean forest-savanna mosaic, an ecoregion of West Africa. Landcover data from 1978 and 1993 showed a reduction of most of Guinea-Bissau's habitats (Table 1). Recently, analyzing Landsat satellite imagery from 1990 to 2007, Oom et al. (2009) suggested that the country's forests had suffered a 1.17% decrease per year, contrasting with an increase of 0.76% and 0.83% of savannah-woodland and mangrove, respectively. These estimates are in line with those reported by the Food and Agriculture Organization (FAO) for West Africa (FAO 2012). Oom et al. (2009) also reported that during that time period 50% of dense forest had already been replaced by open forest, and 13% of open forest converted to

savannah-woodland. Slash-and-burn agriculture and cashew plantations have been the main causes for forest reduction, and the former is also linked with the increase in savannah-woodland, whereas the abandonment of mangrove swamp rice fields led to an increase in the area of mangroves (Oom et al. 2009). Most of the dense forest is located in southern Guinea-Bissau, confined to the regions of Tombali and Quinara which harbor most of the country's biodiversity (Gippoliti and Dell'Omo 1996, Sousa et al. 2005, Torres et al. 2010) (Figure 2).

Table 1. Comparison of Guinea-Bissau landcover estimates (in hectares) from 1978 and 1993 (Source: Programa de Nações Unidas para Desenvolvimento; http://www.didinho.org/).

HABITAT	SCET-INTERNATIONAL (1978)	GEOSYSTEMES (1993)
Secondary or degraded forest	1.076,000	472,094
Dry or semi-dry forest	859,000	647,985
Mangrove	287,000	250,761
Agricultural areas and settlements	276,600	317,414
Herbaceous savannah (*lala*)	160,000	123,691
Rice fields (*bolanhas*)	72,400 (*lala*) +116,000 (mangrove)	170,868
Dense canopy forests	129,000	126,278
Oil-palm plantations	111,800	109,389
Gallery forests	80,000	67,625
Savannah-woodland	51,400	56,232
Tannes*	37,600	94,201
Transition forest	24,000	24,419
TOTAL	2.816,265	2.460,930

*Flat salt marshes comprised of bare soil with salt development or halophilic and hydrophilic herbaceous vegetation.

The rich faunal biodiversity of Guinea-Bissau was first assessed by Monard in 1936, and later by Fernando Frade during an expedition between 1945-46 (Gippoliti and Dell'Omo 2003). Gippoliti and Dell'Omo (2003) listed 10 primate species for Guinea-Bissau and adjacent countries: western chimpanzee (*Pan troglodytes verus*), western black-and-white colobus (*Colobus polykomos*), Temminck's red colobus (*Piliocolobus badius temminckii*), Guinea baboon (*Papio papio*), Green monkey (*Cercopithecus sabaeus*), Campbell's monkey (*Cercopithecus mona campbelli*), Lesser spot-nosed monkey (*Cercopithecus petaurista buettikoferi*), Patas monkey (*Erythrocebus patas*), Sooty mangabey (*Cercocebus atys atys*)

and Senegal bushbaby (*Galago senegalensis*) (Figure 3, Appendix I). Hunting for bushmeat consumption is a major threat to primate populations, and recently Minhós et al. (2013) reported that six of these 10 primate species are regularly hunted, with a minimum estimate of 1550 individuals per dry season, based on DNA barcoding. The green monkey (*C. sabaeus*) revealed to be the most hunted primate in this country (Minhós et al. 2013).

The presence of chimpanzees in the country is only confirmed for three protected areas: LCNP, CNP and BNP (Figure 1-2). The principal threats that chimpanzees face are: human population increase and encroachment; deforestation, mainly associated with the expansion of plantations of cashew or other crops (e.g. rice cultures) and selective logging (e.g. *Borassus aethiopium*); slash and burn agriculture; and the future construction of the Port of Buba in LCNP and mining exploitation in BNP (Casanova and Sousa 2006, 2007, Salgado et al. 2009, Asperbras 2010).

Decree No. 21/1980 provides legal protection of wildlife from hunting. Several ethnic groups, particularly Muslims, regard chimpanzees as too closely resembling humans, and due to these similarities chimpanzees are not hunted for meat (Gippoliti and Dell'Omo 2003, Brugiere et al. 2009), a taboo that also has been reported for the neighboring Republic of Guinea (Sugiyama and Soumah 1988). However, despite legal protection of chimpanzees and a certain level of tolerance by locals, increasing human encroachment has led to a steady rise in human-chimpanzee conflicts, which may ultimately have a negative impact chimpanzee populations (Hockings and Humle 2003, Hockings and Sousa 2011). A transnational interest in chimpanzee skin was reported as an additional threat for the conservation of this species (Sá et al. 2012).

Figure 3. Primate species listed for Guinea-Bissau: a) *Pan troglodytes verus*; b) *Colobus polykomos*; c) *Piliocolobus badius temminckii*; d) *Papio papio*; e) *Cercopithecus sabaeus*; f) *Cercopithecus mona campbelli*; g) *Cercopithecus petaurista buettikoferi* (http://www.apus.ru/site.xp/053057056124050050053050.html); h) *Erythrocebus patas*; i) *Cercocebus atys atys* (Photo: Kathelijne Koops); and j) *Galago senegalensis* (Photo: R. A. Barnes). For English common names and creole names see Appendix I.

1.6.2 Lagoas de Cufada Natural Park (LCNP)

LCNP (located between 11º34' and 11º51' N and 14º49' and 15º16'W) covers an area of 890 km^2 and was created in December 2000 (IBAP 2007, 2008). It is known for its rich biodiversity and is a RAMSAR Convention site (IBAP 2008), with three main lagoons, Cufada (190 ha), Bionrá (13 ha), and Bedasse (8 ha), representing permanent freshwater ecosystems (Catarino et al. 2002). 11000 people belonging to different ethnic groups live inside the park (IBAP 2008), and rely extensively on the park's natural resources for their survival. IBAP as well as other non-governmental organizations (e.g. Palmeirinha) have worked together to keep park residents informed about the importance of forest biodiversity and its sustainable use, even before the official establishment of LCNP as a protected area.

The climate is characterized by a marine influence, i.e. small daily and seasonal thermal fluctuations, with an average temperature of about 26 ºC during both the dry and rainy season. Annual rainfall averages 2200 mm, which mostly falls in the rainy season between June and October, with almost no precipitation (<100 mm) in the pronounced dry season between November and May (Catarino et al. 2002; http://sdwebx.worldbank.org/climateportal/index.cfm). The topography is relatively flat, reaching a maximum of 39 m of altitude, and soil composition and its depth varies, which defines and limits the presence of tree species (Catarino et al. 2006b).

The most relevant plant physiognomic formations are dense and open canopy forests (9.27% and 34.60%, respectively), savannah-woodland (52.37%), and mangroves (1.41%) (Catarino et al. 2006a, Catarino et al. 2006b, Amaro 2011). The habitat types suitable for chimpanzees are dense and open canopy forests, and savannah-woodland. Dense canopy forests are structurally and compositionally similar to the multi-storeyed forests of Sierra Leone and Liberia (FAO 1995). This habitat is found in areas with relatively steep slope and is characterized by a dense canopy that intercepts around 90% of sunlight and is composed of two tree layers, one at 15-20 m and another at 25-40 m (Catarino et al. 2006b). The most common species are *Afzelia africana*, *Albizia* spp., *Antiaris toxicaria*, *Ceiba pentandra*, *Chlorophora* spp., *Detarium senegalense*, *Dialium guineense*, *Elaeis guineensis*, *Erythrophleum guineense*, *Malacantha alnifolia*, *Parkia biglobosa*, *Parinari excelsa* and *Spondias mombin* (FAO 1995, Catarino et al. 2006b) (see Appendix II). Open canopy forests

have been subject to greater levels of human disturbance, particularly slash and burn agriculture. The canopy cover is about 60-70%, and two distinct canopy layers can also be found, however, at lower heights than in dense forests (8-15 m and 15-20 m). These forests are widely represented by *Borassus aethiopium*, *Daniellia oliveri*, *P. biglobosa* and *Piliostigma thonningii*. Open forests and savannah-woodlands have some tree species in common due to their occurrence on similar soil types (Catarino et al. 2006b). Only one layer of arboreal canopy is found at 10-12 m, with canopy coverage of about 20-40%. Other tree species are restricted to savannah: *Albizia zygia*, *Combretum* spp., *Crossopteryx febrifuga*, *Ficus* spp., *Lophira lanceolata*, *P. thonningii*, *Pterocarpus erinaceus*, and *Terminalia albida*. Herbaceous climbers are found in all three habitat types, *Dioscorea* spp. being the most common, whereas liana species of the genera *Landolphia* and *Combretum* are restricted to forest habitats (Catarino et al. 2006b) (see Appendix II).

Before 2008, evidence suggested that chimpanzees occurred in the forests surrounding 23 villages inside LCNP (Casanova and Sousa 2007). In other park areas, chimpanzees were seriously threatened by deforestation and human population increase and/or there was no evidence of their presence (Casanova and Sousa 2007). Since 2008, the situation has become worse: Bauxite Angola S.A. illegally deforested more than half of the primary forest and opened a large road inside the park (Salgado et al. 2009). This company intends to implement a mining project in Boé National Park to explore bauxite and to build a harbour inside LCNP to facilitate bauxite exportation (http://www.geoport.eng.br/buba2.html). Nowadays, the company GEOPORT seems to be responsible for this project (see http://www.geoport.eng.br/buba1_ing.html).

In 2011, information was obtained about a future local project that intends the large-scale exploitation of fruits of *D. guineense* (Nelson Dias, personal communication). This is a reason for concern since the fruits of this tree species are among the ones most consumed by chimpanzees during part of the year (February-June), and consequently this may contribute to increasing chimpanzee-human conflicts (Kormos et al. 2003, Casanova and Sousa 2007).

1.7 Aims and outline of the dissertation

The main aim of this dissertation was to assess population density and abundance, habitat use, nesting and feeding preferences of chimpanzees living in a forest-savannah mosaic widely disturbed by humans. In particular, chimpanzee populations of LCNP were chosen because they represent the westernmost margin of the subspecies' geographic distribution, and ecological information on *P. t. verus* from Guinea-Bissau is still scant. The study also intended to contribute valuable data to future assessments of the conservation status of *P. t. verus*.

In *Chapter 1* a general introduction to the aims covered throughout this dissertation is presented. Specifically, a brief introduction to the anthropogenic disturbances associated to biodiversity loss and fragmentation of several primate habitats worldwide is given, with a particular focus on chimpanzees. The most recommended sampling designs and methodologies to estimate chimpanzee population density and size are described. Further, the cultural, ecological and environmental contexts related to chimpanzee nesting and feeding are briefly outlined to improve insights into the determinants of spatio-temporal variation of chimpanzee distribution and habitat use and selection. Finally, the representativeness of vegetation types and primate species listed for Guinea-Bissau as well as a description and relevant information of the study area are given.

Chapter 2: Chimpanzee density and abundance and human disturbances

As outlined above, the biodiversity of LCNP has been severely affected by destructive human activities such as agriculture, logging, and poaching. In 2008, biodiversity was further put at risk by an increase in illegal logging of primary forest, seriously compromising the availability of suitable chimpanzee habitat inside the park. Employing nest count surveys and distance-sampling methods, the main aim of this chapter was to provide density and population size estimates for LCNP chimpanzees after the illegal logging. Patterns of chimpanzee nest occurrence in relation to a set of landscape-scale variables which can be regarded as proxies for human disturbance, namely principal rivers, roads (including main and secondary roads), and human settlements, were also assessed.

The findings presented in this chapter were published in the following paper:

1. Carvalho J. S., Marques T. A. and Vicente L. 2013. Population status of *Pan troglodytes verus* in Lagoas de Cufada Natural Park, Guinea-Bissau. *PLoS ONE*. 8(8): e71527. (DOI: 10.1371/journal.pone.0071527).

Chapter 3: Chimpanzee Nesting Patterns

Anthropogenic activities such as logging and agriculture profoundly alter structural and compositional aspects of primate habitats worldwide. Identification of the principal vegetation correlates of primate occurrence is important to help guide conservation action, yet few studies to date have quantitatively examined how vegetation characteristics affect abundance and distribution patterns of chimpanzees. Considering nest count surveys and a quantitative assessment of the vegetation, the main aim was to investigate the ecological determinants of chimpanzee distribution at the habitat and nest tree species scale. Particularly, the vegetation correlates of chimpanzee nest abundance in LCNP were assessed. Patterns of nest height distribution were also investigated to evaluate evidence for or against the anti-predation hypothesis, which posits that chimpanzees at sites with predators built nests consistently higher than at those with low predation pressure. At the tree species scale, patterns of nest tree species selection were assessed to further our understanding of how this behaviour varies geographically across the species' range.

This chapter has originated one paper:

2. Carvalho J. S., Meyer C. F. J., Vicente L., and Marques T. A. 2014. Where to nest? Ecological determinants of chimpanzee nest abundance and distribution at the habitat and tree species scale. *Am. J. Primatol.* In press.

Chapter 4: Chimpanzee Diet and Food Availability

Food availability determines the spatial and temporal distribution, habitat use, and diet diversity and composition of chimpanzees. Combining data on plant phenology with the analysis of faecal samples and feeding remains, the main goal of this chapter was to assess the spatio-temporal variation in food availability and dietary diversity and composition of LCNP chimpanzees. Particularly, the spatial and temporal variation of dietary composition was investigated among habitats and over the dry season, respectively. The temporal variation of

dietary richness and diversity was also assessed in relation to fruit availability over the dry season.

This chapter has originated one paper:

3. Carvalho J. S., Vicente L., and Marques T. A. Spatio-temporal variation in chimpanzee food availability and dietary composition in a human-dominated landscape. Submitted.

Chapter 5 consists of a general discussion, in which the major findings of this thesis are integrated. Methodological implications of this research for future chimpanzee population assessments are also highlighted, and the implications of this work for chimpanzee conservation in Guinea-Bissau discussed. Finally, prospects for future work are outlined.

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Chapter 2

Chimpanzee Density and Abundance and Human Disturbances

Resumo - O chimpanzé ocidental, *Pan troglodytes verus*, encontra-se classificado com o estatuto de "ameaçado" desde 1988 segundo a lista vermelha da IUCN. Doenças infecciosas e/ou várias actividades humanas tais como a desflorestação, agricultura de larga escala, caça ilegal e exploração mineira, têm sido apontadas como as principais causas do declínio do efectivo populacional de *P. t. verus*. Como várias populações de chimpanzés encontram-se distribuídas por paisagens antropogénicas, é urgente estimar e monitorizar o tamanho e a distribuição destas populações, assim como avaliar o seu estatuto de conservação. Deste modo, estimou-se a densidade e tamanho populacional dos chimpanzés do Parque Natural das Lagoas de Cufada (PNLC, Guiné-Bissau), uma área protegida dominada por actividades humanas. Apesar de alguns estudos terem analisado a distribuição de chimpanzés em relação a diferentes níveis de perturbação humana, poucos foram aqueles que providenciaram uma quantificação detalhada desta relação. Assim, padrões de ocorrência dos chimpanzés do PNLC relativamente a covariáveis de perturbação humana à escala da paisagem, tais como vilas, estradas e rios, foram explorados. Métodos de amostragem por distâncias e contagem individual de ninhos foram aplicados ao longo de 11 transectos lineares sistematicamente distribuídos, durante a estação seca de 2010 e 2011. A estimativa da taxa de decaimento dos ninhos foi de 293 dias (%CV=58.8), próxima das estimativas documentadas para outras populações de *P. t. verus*. Considerando o método *Standing-Crop Nest Count* a estimativa da densidade para 2011 foi de 0,22 chimpanzés que constroem ninhos/ km^2 (95% IC: 0,08-0,62), correspondendo a 137 chimpanzés (95% IC: 51.0-390.0) no PNLC. Em comparação com outras populações de chimpanzés na Guiné-Bissau, a menor densidade parece encontrar-se no PNLC. Neste parque, a maior densidade de chimpanzés foi estimada para o habitat menos disponível, i.e. floresta de canópia densa, realçando uma preferência pela floresta com maior cobertura de canópia para a construção de ninhos. As covariáveis de perturbação humana revelaram influenciar negativamente a distribuição dos chimpanzés do PNLC, verificando-se uma elevada abundância de ninhos longe de vilas, estradas e rios, coincidindo com a distribuição dos fragmentos de floresta densa. A fragmentação e perda constante e continuada das áreas florestadas adequadas à sobrevivência do chimpanzé (p.e. a substituição da floresta densa por plantações de cajú) parecem estar a comprometer a distribuição das populações de chimpanzés

do PNLC. Recomendações e estratégias de conservação a longo prazo de *P. t. verus* e dos fragmentos florestais são discutidas.

Palavras-chave: amostragem por distâncias; chimpanzé ocidental; contagem individual de ninhos; perturbação humana; tamanho e densidade populacional; transectos lineares.

Paper I. Population status of *Pan troglodytes verus* in Lagoas de Cufada Natural Park, Guinea-Bissau

Carvalho J. S., Marques T. A. and Vicente L. 2013. *PLoS ONE*. 8(8): e71527. (DOI:10.1371/journal.pone.0071527).

Abstract - The western chimpanzee, *Pan troglodytes verus*, has been classified as Endangered on the IUCN Red List since 1988. Intensive agriculture, commercial plantations, logging, and mining have eliminated or degraded the habitats suitable for *P. t. verus* over a large part of its range. In this study we assessed the effect of land-use change on the population size and density of chimpanzees at Lagoas de Cufada Natural Park (LCNP), Guinea-Bissau. We further explored chimpanzee distribution in relation to landscape-level proxies of human disturbance. Nest count and distance-sampling methods were employed along 11 systematically placed linear transects in 2010 and 2011. Estimated nest decay rate was 293.9 days (%CV=58.8). Based on this estimate of decay time and using the Standing-Crop Nest Count Method, we obtained a habitat-weighted average chimpanzee density estimate for 2011 of 0.22 nest building chimpanzees/km^2 (95% CI 0.08-0.62), corresponding to 137 (95% CI 51.0-390.0) chimpanzees for LCNP. Human disturbance had a negative influence on chimpanzee distribution as nests were built farther away from human settlements, roads, and rivers than if they were randomly distributed, coinciding with the distribution of the remaining patches of dense-canopy forest. We conclude that the continuous disappearance of suitable habitat (e.g. the replacement of LCNP's dense forests by monocultures of cashew plantations) may be compromising the future of one of the most threatened Guinean coastal chimpanzee populations. We discuss strategies to ensure long-term conservation in this important refuge for this chimpanzee subspecies at its westernmost margin of geographic distribution.

Key-words: western chimpanzee; human disturbance; line transect distance sampling; nest count methods; strip transects; population size; population density.

2.1 Introduction

In the last decades, primate populations have suffered great demographic declines (Walsh et al. 2003, Campbell et al. 2008). These declines are due to several reasons, all having human activities and/or infectious disease epidemics as their core basis. However, little is known about how these threats translate into actual decrease in population size. Poaching, pet trade, slash-and-burn agriculture, deforestation associated with logging and agricultural activities, large-scale agricultural plantations, and other threats explain the biodiversity loss and fragmentation of several primate habitats worldwide (Gippoliti and Dell'Omo 2003, Sá et al. 2012).

On the large scale distribution patterns of species are shaped by environmental and historical constraints (Lehman and Fleagle 2006, Kamilar 2009, Harcourt and Wood 2012). On the small scale behavioural characteristics including territoriality, location of nesting sites, predation, and competition for food or mates determine where a species is found (Nkurunungi and Stanford 2006). Today, human disturbance, quantifiable by population density, socio-economic and cultural factors, and the extent of roads and highways (Fa et al. 2002, Yackulic et al. 2011, Vanthomme et al. 2013), is one of the major determinants of wildlife distributions (Paudel and Kindlmann 2012), including chimpanzees (Torres et al. 2010, Junker et al. 2012). Primate distributions in Africa have been greatly affected by the expansion of road networks (Blom et al. 2001, Baldé 2008), not only providing access to settlers but facilitating illegal hunting and logging (Hashimoto 1995, Devos et al. 2008, Vanthomme et al. 2013). In West and Central Africa, hunting is one of the greatest threats due to the dependence of local populations on bushmeat, for subsistence and for commerce (Oates 1996, Kuehl et al. 2009, Linder and Oates 2011). Rivers can act as natural barriers shaping primate distribution patterns (Harcourt and Wood 2012, Inogwabini et al. 2012), while at the same time allow for an easy transport of bushmeat (Fa et al. 2002).

Many studies have analyzed primate distributions with respect to different levels of human disturbance (Tutin and Fernandez 1984, Oates 1996, Hall et al. 1998, Pusey et al. 2008), but few have provided a detailed quantification of the relationship (Lahm et al. 1998, Stokes et al. 2010, Torres et al. 2010, Junker et al. 2012). The impact of human activities on chimpanzee populations has been evaluated over large areas (Stokes et al. 2010, Junker et al. 2012), but there are few quantitative studies that have been conducted at a small geographic scale (Kuehl et al. 2009, Torres et al. 2010, Vanthomme et al. 2013).

The western chimpanzee *Pan troglodytes verus* has been listed as Endangered on the IUCN Red List since 1988 (IUCN 2014). *Pan t. verus* has, nonetheless, undergone a considerable population reduction over the last 20 to 30 years (Boesch and Boesch-Achermann 2000). Its range encompasses nine West African countries, although it is already considered rare or close to extinction in four of them: Burkina-Faso, Ghana, Guinea-Bissau, and Senegal (Kormos et al. 2003). Junker et al. (2012) carried out a meta-analysis for eight taxa of African great apes that assessed continent-wide suitable environmental conditions and how they had changed over 20 years. They found that the western chimpanzee had suffered a decline of 11% in the area of suitable environmental conditions since 1992. The Cantanhez National Park in Guinea-Bissau has suffered the same loss of chimpanzee habitat (11%) since 1986 (surveys in 1986, 1994 and 2003; (Torres et al. 2010)).

Population estimates for this subspecies range from 21,300 to 55,600 individuals (Kormos et al. 2003), with 600-1000 individuals in Guinea-Bissau (Gippoliti and Dell'Omo 2003). Questionnaire surveys suggest that the range of chimpanzees is restricted by humans (Brugiere et al. 2009). In Guinea-Bissau, the highest human population densities are found in the north of the country (http://www.bestcountryreports.com/Population_Map_Guinea-Bissau.php) and suitable habitat for *P. t. verus* is found only in the south (Torres et al. 2010); in the south-west, in the region of Tombali, including the Cantanhez Forest and Cacine Basin, and in the region of Quinara, particularly in Lagoas de Cufada Natural Park (LCNP), and in the east in Boé (Figure 1) (Gippoliti and Dell'Omo 1996, Sousa et al. 2005).

The first report on the status of *P .t. verus* in this country dates from 1940 (Monard 1940 *in* (Gippoliti and Dell'Omo 1995)) and only recently have studies provided updated assessments (Casanova and Sousa 2005, Sousa et al. 2011), which, however, have focused only on a small area of the country or have employed a less robust study design (Sousa et al. 2005, Brugiere et al. 2009, Sousa et al. 2011) than is recommended (Buckland et al. 2001). For LCNP, the evidence available before 2008 suggests that chimpanzees occurred in the forests surrounding 23 villages, while in other areas they were scarce and seriously threatened by deforestation, poaching and increasing human populations, in others there were no signs at all of their presence (Casanova and Sousa 2007). No reliable estimates of the current population size and density of *P.t verus* in this important protected area were available.

In this paper, we provide robust density and population size estimates for the western chimpanzee population in LCNP using a distance-sampling approach (Buckland et al. 1993, Buckland et al. 2001). We also assess patterns of chimpanzee occurrence inside LCNP in relation to landscape-scale covariates of human disturbance, such as roads, rivers, and settlements.

2.2 Methods

Ethics statement

All research was conducted under permissions from *Instituto da Biodiversidade e Áreas Protegidas* (IBAP), Guinea-Bissau. No animals were captured or handled during this study.

Study site

Guinea-Bissau is a small (36,125 km^2) West African country (Figure 1) with relatively flat topography (Gippoliti and Dell'Omo 2003). Patches of primary forest remain in the north-west and south-west of the country, in the regions of Cacheu, Quinara, and Tombali (Gippoliti and Dell'Omo 2003). Landscape satellite images have shown, however, that dense-canopy forests continue to decline in extent and number, being replaced by open-canopy forests and savannah-woodland (Oom et al. 2009, FAO 2012) (Table S1). The dense-canopy forests are being replaced by subsistence farming of rice, sugarcane and maize, and cashew plantations (Oom et al. 2009).

LCNP is located in the region of Quinara, in southern Guinea-Bissau, between 11º34' and 11º51' N and 14º49' and 15º16' W (Figure 1) (Catarino et al. 2006a, Catarino et al. 2006b). The climate is characterized by an average annual temperature of 26ºC and an average annual rainfall of 2200 mm, with a pronounced rainy season from June to October/November (Catarino et al. 2002). LCNP is an internationally recognized Ramsar site and covers an area of 890 km^2 (Sousa et al. 2005). It is managed by a governmental organization, the *Instituto da Biodiversidade e das Áreas Protegidas* (IBAP). IBAP faces severe funding and personnel limitations despite multiple threats to the park's integrity. Different ethnic groups (around 11,000 people) live in the park, relying extensively on natural resources for their survival. The

villages are close to roads or water sources (rivers or lagoons). The villagers' livelihoods depend on subsistence farming, and bushmeat hunting is common.

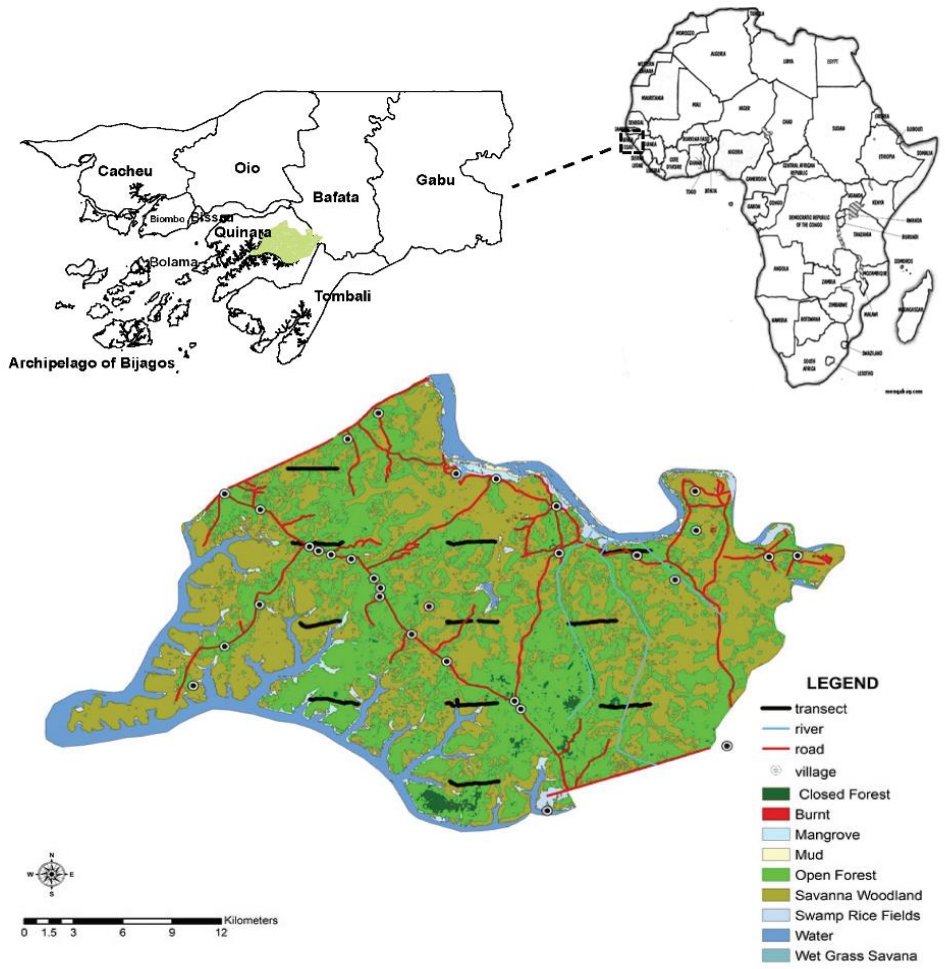

Figure 1. Location of the 11 linear transects inside the protected area Lagoas de Cufada Natural Park. The location of the Republic of Guinea-Bissau and respective administrative regions is shown. doi:10.1371/journal.pone.0071527.g001

Chimpanzee nest surveys

As chimpanzees in LCNP are not habituated to humans and, as such, very elusive (only 10 encounters were recorded in 2011), we relied on nest surveys for estimating population densities (Ghiglieri 1984, Tutin and Fernandez 1984, Hashimoto 1995, Furuichi et al. 2001).

Nest counts are a useful surrogate for estimating ape densities and monitoring their populations over time (Kühl et al. 2008, Buckland et al. 2010a). Most studies recommend using line transect surveys (Blom et al. 2001, Buij et al. 2002, Devos et al. 2008, Fleury-Brugiere and Brugiere 2010), during which all the nests visible from the transect line are counted either individually (Ghiglieri 1984, Hashimoto 1995) or in groups (Tutin and Fernandez 1984), or both (Furuichi et al. 2001). Two nest count techniques are recommended: Standing-Crop Nest Counts (SCNC) and Marked Nest Counts (MNC). SCNC consists of only a single visit to all transects, counting all nests irrespective of their age class, whereas MNC consists of counting only nests built between successive visits to the same transect, with all nests removed in the first visit, within an interval short enough to guarantee that no new nests will disappear between repeated visits. SCNC is logistically easier (Tutin and Fernandez 1984, Plumptre and Reynolds 1996, Blom et al. 2001, Fleury-Brugiere and Brugiere 2010), although it requires independent estimates of rates of nest production and nest decay. MNC, on the other hand, is the only alternative when nest decay rate is lacking (Hashimoto 1995, Plumptre and Reynolds 1996, Furuichi et al. 2001, Devos et al. 2008). The pros and cons of these methods are well described in the literature (Devos et al. 2008, Kühl et al. 2008).

Here, we used a hybrid approach, depending on survey year, sampling unit, and nest count method. We estimated (1) densities of chimpanzee nests for 2010 and 2011 using line transect surveys and SCNC, (2) chimpanzee density for 2010 using strip transect surveys and MNC, (3) nest decay rate in 2010 for LCNP, and (4) subsequently, based on line transect sampling and SCNC, the chimpanzee density for 2011 using our estimate of nest decay rate and published information on nest production rate.

Following the recommendations for an adequate study design (Buckland et al. 1993, Buckland et al. 2001), 11 linear transects (each one 3 km long) were superimposed over LCNP as a grid of equally-spaced (5 x 6km) parallel lines (Figure 1). Our design adhered to the assumptions underlying distance sampling (Buckland et al. 2001).

All field work was conducted by JC, during 10 months in the dry seasons of 2010 and 2011. Habitat types along each line transect were classified based on canopy coverage as either dense-canopy forest, open-canopy forest, or savannah-woodland (Catarino et al. 2002, Catarino et al. 2006b) and geo-referenced to calculate the exact proportion of each in these sampling units. Line transects were visited four and five times, respectively, in 2010 and 2011, at biweekly

intervals. The transects were walked at a steady speed of about 1 km/h (Plumptre and Reynolds 1996, Furuichi et al. 2001).

Only data on individual nests were collected, considering that nest groups were hard to identify as nests showed the highest aggregation in dense-canopy forests. Whenever a nest was found, the perpendicular distance from the transect line to the nest was measured with a tape measure or range finder (Bushnell Yardage Pro Sport 450). To avoid double counting, nest trees were tagged with a rope. Nests observed during the 2011 survey were geo-referenced using a Global Positioning System (GPS Garmin 60) (only one reading was taken when there were several nests close to each other in the same tree).

Analyses

Distance sampling nest surveys

We used the software DISTANCE 6.0 (Thomas et al. 2010) to estimate nest encounter rate, the nest detection function, and the densities of nests and chimpanzees. We first explored the distance data in histograms, considering different cut-off points and fitting a half-normal model without adjustment terms to get a first feel for the shape of the detection function and to assess the best truncation distance (*w*). Some data truncation is recommended to avoid problems fitting the tail of the distribution, and 5% has been recommended as a plausible omnibus value for *w* (Buckland et al. 2001). Subsequently, we considered a range of other models implemented in DISTANCE to assess which model provided the best fit to the data. The best model was selected using Akaike's Information Criterion (AIC), and by evaluating the goodness of fit of the models based on the standard chi-square, the Kolmogorov-Smirnov and the Cramér-von Mises tests (Buckland et al. 2001).

Estimation of nest densities from line transects using SCNC

Only nest data from the first visit to any particular transect in each year were used to obtain the nest detection function by habitat. We opted not to include data from subsequent visits for nest density estimation because, even under the assumption that during biweekly intervals no newly built nest will disappear, old nests were detected during repeated visits (Furuichi et al. 2001).

Nest data were examined following the procedures described above for model selection and model evaluation. First, we estimated nest densities for each habitat. Nest density D_n was estimated using the conventional distance sampling estimator as

$$\hat{D}_n = \frac{n\hat{f}(0)}{2L} \quad , \qquad (1)$$

where *n* represents the number of the detected nests, $\hat{f}(0)$ is the estimated probability density function of detected nests evaluated at distance 0 and *L* is the total length of transects (Buckland et al. 2001). Global nest density was obtained as a weighted average of habitat specific estimates, with weights given by habitat area.

Estimation of chimpanzee density and nest decay rate from strip transects using MNC

The linear transects were also regarded as constituting a grid of randomly positioned strips. Unlike line transect sampling, standard strip transect sampling assumes that all objects (either individuals or indirect evidence of their occurrence) within a distance *s* along transects are detected, and providing a large enough sample size an unbiased estimator of density and precise estimates of abundance can be obtained (Blom et al. 2001, Ogutu et al. 2006, Buckland et al. 2010b). To maximize the likelihood of detecting all nests within distance *s*, we used the 2010 dataset considering only nests from the second visit onwards to find the distance *s* for which we could consider that all new nests were detected, i.e., that would allow us to define sensible strip transects. The width of strip transects (*s*) was defined by the distance over which the shoulder of the detection function extended. We considered habitat-specific strip transects, given that the width over which it is reasonable to assume that all nests are detected was expected to be habitat dependent (compare also (Chapman et al. 1988)).

Following data exploration as described above, we estimated chimpanzee density by habitat, and then global density weighted by habitat, as

$$\hat{D} = \frac{n}{2Lst\hat{r}} \quad , \qquad (2)$$

where *n* represents the number of new nests detected within the strip transect from the second visit onwards, *L* is the total strip transect length, *s* is the width of the strip transect (taken from the shoulder of the detection function as described above), *t* is the number of days elapsed between the first and last survey, and $\hat{r}$ is the daily nest production rate (Buckland et al. 2001). As an estimate of nest production rate for our study area or Guinea-Bissau is lacking, we used a published estimate of 1.143 nests built per animal per day (%CV=3.51) from Taï National Park, Ivory Coast (Kouakou et al. 2009). 95% confidence intervals for nest encounter rates and density estimates were calculated in R version 2.15.3 (R Development Core Team 2013) using a nonparametric bootstrap procedure (999 resamples).

Using the above 2010 estimates of nest density and chimpanzee density, we subsequently obtained an estimate of nest decay rate by rearranging the following equation and solving it for $\hat{d}$

$$\hat{D} = \frac{\hat{D}_n}{\hat{d}\hat{r}} \quad , \tag{3}$$

where $\hat{D}_n$ denotes the estimate of nest density, $\hat{d}$ is the nest decay rate (days) and $\hat{r}$ is the nest production rate per day (Buckland et al. 2001). Nest decay rate was calculated for 2010.

The variance for the decay rate estimator can be approximated via the delta method (Powell 2007) as

$$\mathrm{var}(\hat{d}) \approx d^2 \left\{ CV(\hat{D}_n)^2 + CV(\hat{D})^2 + CV(\hat{r})^2 \right\} \quad , \tag{4}$$

where *CV* represents the coefficient of variation of the corresponding estimate, i.e., the standard error of the estimate divided by the estimate.

Estimation of chimpanzee densities from line transects using SCNC

Based on the estimated rate of nest decay and again using the estimate of the daily rate of nest production from Taï National Park, we were able to apply the SCNC technique (Plumptre and Reynolds 1997) to estimate a habitat-weighted average of chimpanzee densities using equation 3 for the 2011 data.

Relationship between nest distribution and landscape-scale covariates

Nests were used as an indirect measure of the presence of chimpanzees (Torres et al. 2010). A randomization test was performed using the package *COIN* in R version 2.15.3 (R Development Core Team 2013) to assess relationships between the spatial distribution of chimpanzee nests and a set of landscape-scale variables which can be regarded as proxies for human disturbance: principal rivers, roads (including main and secondary roads), and human settlements. To determine whether nests were distributed in a non-random fashion with respect to these variables we compared the mean distances between nest locations and each environmental feature to mean distances generated in the same way based on random locations of 214 (number of independent nest locations in the data) nests within transects. This procedure was repeated 1000 times and statistical significance was assessed by recording the number of times the mean value from random locations was lower than the observed value for nest locations (Manly 1997). We used the Geographic Information System (GIS) ARCMAP 9.3 package to calculate the shortest straight-line distance between each nest and a given environmental feature. All spatial layers were projected into Universe Transverse Mercator (UTM) Zone 28N. Environmental digital data were made available through the CARBOVEG project (http://carboveg-gb.dpp.pt/) or taken from Amaro (2011). To ensure that sampling of random points (n=214) fell within the area surveyed, a buffer was constructed along both sides of the transects and limited by the maximum distance at which a nest was observed from the transect line surveys (84m). In addition, to investigate the distribution of habitats in relation to the environmental features considered, we also plotted the measured distances grouped by habitat type and tested for statistical differences.

2.3 Results

Chimpanzee nest surveys

Survey effort for SCNC was 67.2 km, whereas 235.2 km were walked for MNC. Line transects were composed mostly of savannah-woodland (46.81%), followed by dense-canopy forest (26.28%), open-canopy forest (9.97%), agricultural areas (10.08%), herbaceous savannah (5.35%), rivers or lagoons (1.23%) and human settlements (0.28%) (Figure S1). These relative proportions of habitat types in LCNP constitute a good representation of their occurrence countrywide (Table S1). In 2010, 211 nests were detected, 182 of them during the first visit. A

total of 248 nests were recorded in 2011, 117 of those during the first visit. The highest count during the first visit is the natural consequence of nest accumulation over time.

Once corrected for estimated habitat specific detectability (see results below) nests were found mostly in dense forest (71.55 %), and fewer nests were recorded in the two habitats with less canopy coverage: savannah-woodland (17.98%) and open forest (10.48 %). Distances at which nests were detected from the line transect differed significantly among habitat types (Kruskal-Wallis test, $\chi^2 = 40.82$, df=2, p<0.001) (Figure S2), being greatest in savannah and shortest in dense forest.

Estimation of nest densities from line transects using SCNC

Truncating the data at 42 meters, a uniform model with a cosine adjustment provided the best fit for the 2010 dataset (ΔAIC=0.77; the reported values of ΔAIC correspond to the comparison with the second best model unless otherwise noted). Open forests showed the highest nest encounter rate followed by dense forests and savannahs (Table 1). Habitat-specific nest density estimates were substantially higher for open and dense canopy forests compared to savannahs (Table 1). For 2010, the global nest density estimate for LCNP was 167.97 nests per km^2 (95% CI 55.61-507.34).

Table 1. Comparison of nest count, nest encounter rate (nests/km) and nest density estimates (nests/km^2) between 2010 and 2011 of the chimpanzees in Lagoas de Cufada Natural Park.

Year	Survey habitat	No. of nests	Nests/km [95% CI]	Nests/km^2 [95% CI][a]	% CV[b]
2010	Global[c]			167.97 [55.61-507.34]	44.21
	DF	65*	7.37 [1.77-30.64]	229.68 [55.22-955.30]	66.17
	OF	67*	20.03[4.88-82.26]	364.37 [90.07-1,474.10]	54.36
	SAV	36*	2.29 [0.81-6.44]	27.28 [9.70-76.72]	48.20
2011	Global[c]			75.56 [27.21-209.86]	42.22
	DF	72*	8.16 [3.36-19.81]	233.21 [96.02-566.39]	38.87
	OF	17*	5.08 [1.01-25.59]	129.79 [26.39-638.39]	63.52
	SAV	13*	0.83 [0.19-3.52]	11.82 [2.77-50.36]	71.23

[a]CI, confidence interval.
[b]Coefficient of variation.
[c]Average nest density weighted by habitat.
*Distance truncated at 42m (2010) and 35m (2011).
DF- dense canopy forests; OF- open canopy forests; SAV- savannah-woodlands.

Applying a truncation distance of 35 m, a uniform model with a cosine adjustment (Δ AIC=3.06) best fitted the 2011 data. The number of nests observed in dense forests was similar to 2010, whereas far fewer nests were observed in open forests and savannahs, leading to much lower estimates of nest encounter rate for these habitats compared to the previous year (Table 1). Nest density was highest in dense forests, followed by open forests and savannahs, resulting in a global nest density estimate of 75.56 nests per km^2 (95% CI 27.21-209.86) estimated for the entire park, less than half of the previous year's estimate (Table 1). Note, however, the considerable overlap in the 95% CIs, suggesting that this reduction is not statistically significant.

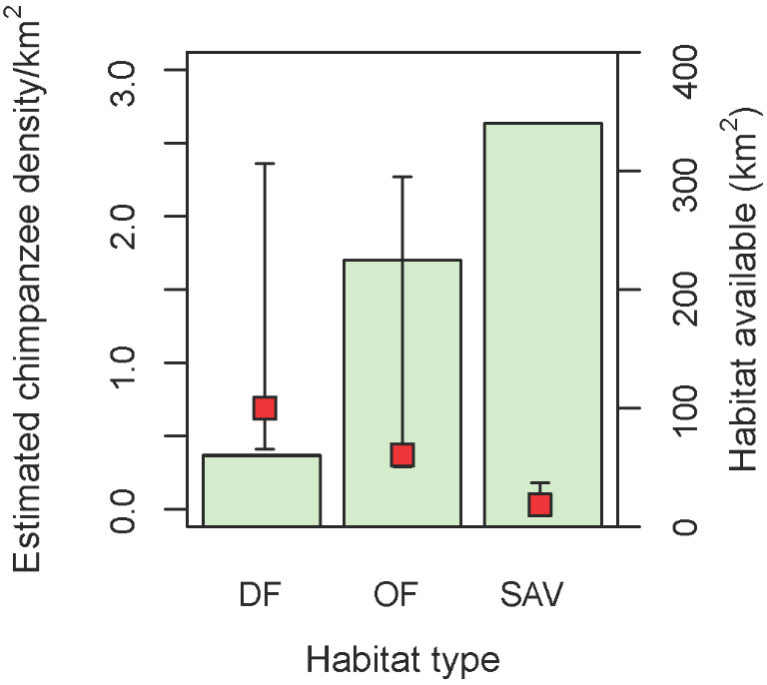

Figure 2. Estimates of chimpanzee density by habitat type for 2011. Estimates were based on line transect surveys, applying the Standing-Crop Nest Counts method. Also indicated is the area occupied by each type of habitat in Lagoas de Cufada Natural Park. Dense canopy forests (DF), open canopy forests (OF) and savannah-woodlands (Sav) were the habitats considered. doi:10.1371/journal.pone.0071527.g002

Estimation of chimpanzee density and nest decay rate from strip transects using MNC

Based on AIC, a half-normal model with cosine adjustment showed the best fit to the 2010 data after truncation at 44 m (ΔAIC=2.08). Based on the detection function, strip transects of different width were obtained for each habitat (Table S2). Habitat-specific density estimates were similar in dense and open forests (Table S2). The park-wide weighted average estimate was 0.50 nest builders per km^2 (95% CI 0.18-1.39), corresponding to about 311 chimpanzees for LCNP. Using these estimates of chimpanzee densities and the nest densities estimated above for 2010 (Table 1), nest decay rate was estimated to be 293.9 days (%CV=58.80).

Estimation of chimpanzee densities from line transects using SCNC

Using the above estimated rate of nest decay, chimpanzee density estimates for 2011 were highest in dense forests and lower in savannahs (Figure 2, Table 2). The habitat-weighted average for LCNP was 0.22 nest builders per km^2 (95% CI 0.08-0.62), corresponding to 137 chimpanzees. It is important to note that the greatest chimpanzee density was estimated for the least available habitat type (Figure 2).

Table 2. Chimpanzee density estimates (builders/km^2) for each habitat and for the Lagoas de Cufada Natural Park obtained in 2011 based on Standing-Crop Nest Counts, using our estimated rate of nest decay.

Survey habitat	Density (builders/km^2)	95% CI[a] (builders/km^2)	%CV[b]
Global[c]	0.22 *	0.08-0.62	42.22
Dense canopy forests	0.69*	0.28-1.67	38.87
Open canopy forests	0.37*	0.08-1.90	64.00
Savannah-woodlands	0.03*	0.01-0.15	71.23

[a]Confidence interval
[b]Coefficient of variation.
[c]Average nest density weighted by habitat.
*results using the nest decay rate of 293.9 days (%CV=58.80).

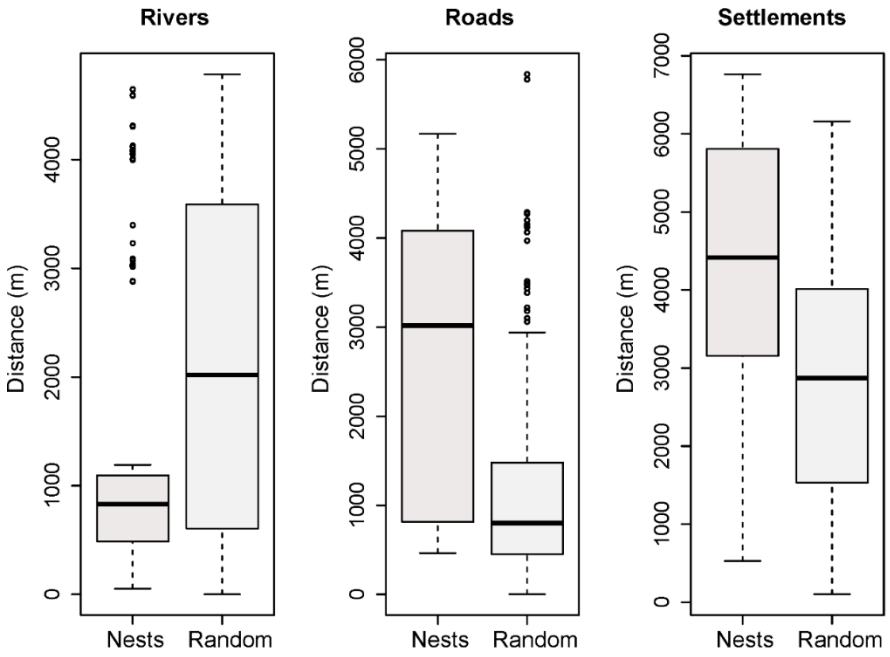

Figure 3. Nearest distances from chimpanzee nests and random points to the landscape-scale covariates. Rivers, roads, and human settlements were considered as proxies of human disturbance. doi:10.1371/journal.pone.0071527.g003

Relationship between Nest Distribution and Landscape-Scale Covariates

The randomization test showed that the spatial distribution of chimpanzee nests differs significantly from a random pattern for all three environmental variables examined. Chimpanzees prefer to build their nests farther away from roads (Z=9.55, p<0.001), settlements (Z=7.60, p<0.001), and rivers (Z=-5.81, p<0.001) than would be expected by chance. On average nests were observed farther away from settlements (4.13 km, 95% CI 3.88-4.37), than from roads (2.58 km, 95% CI 2.37-2.80) or rivers (1.28km, 95% CI 1.10-1.45) (Figure 3).

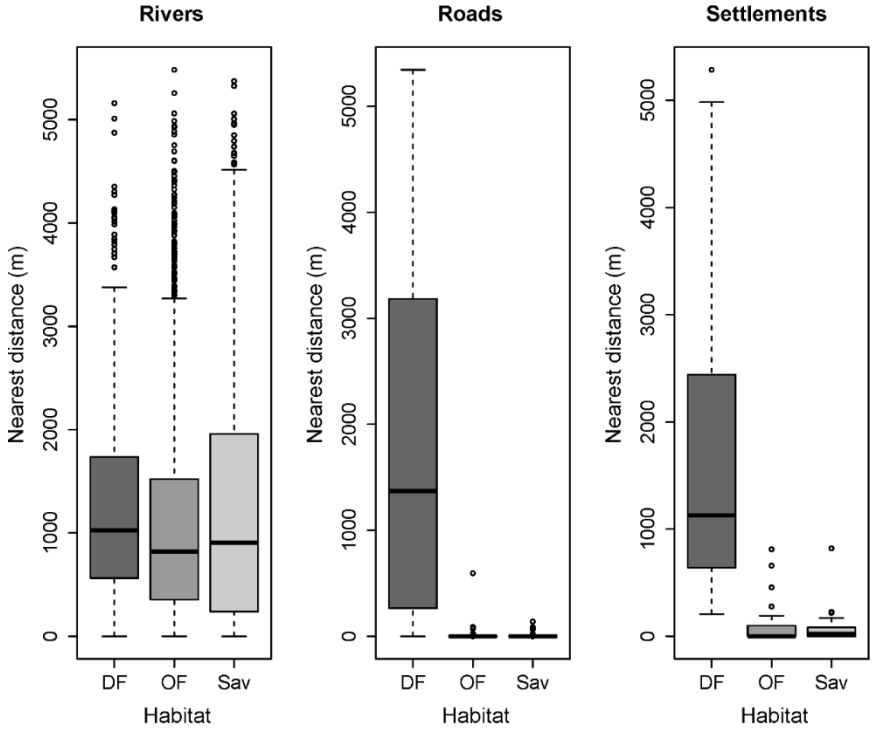

Figure 4. Nearest distances from habitats used by chimpanzees for nest building to the landscape-scale covariates. Rivers, roads, and human settlements were considered as proxies of human disturbance. Dense canopy forests (DF) are located farther from all landscape variables, and shortest distances were obtained for habitats with a lower tree canopy cover, such as open canopy forests (OF) and savannah-woodlands (Sav). doi:10.1371/journal.pone.0071527.g004

The distribution of habitats differed significantly in relation to the environmental features (Kruskal-Wallis test: rivers $\chi^2 = 10.55$, df=2, p<0.05; roads $\chi^2 = 124.29$, df=2, p<0.001; settlements $\chi^2 = 56.89$, df=2, p<0.001), whereby habitats with a lower tree canopy cover (open forests and savannahs) were found closer to all landscape variables, contrasting with the large distances obtained for dense forests (Figure 4).

2.4 Discussion

Chimpanzee population density and size

We presented chimpanzee density estimates at LCNP for 2010 (0.50 nest builders per km^2, 95% CI 0.18-1.39) and 2011 (0.22 nest builders per km^2, 95% CI 0.08-0.62). While it is true that the 95% confidence intervals overlap considerably, hence not suggesting a large population change, we believe the apparent doubling of the point estimates is an artefact (i.e. a consequence of the large CV's associated with these estimates) and these numbers provide nonetheless a good comparison for future studies in this region. By comparison with previous studies for Guinea-Bissau we report the lowest chimpanzee density estimate (Table S3). There are three published studies for this country that provide density estimates based on distance sampling, however, just one of them employed a random sampling of line transects (Sousa 2009) and the remainder used abandoned trails or trails used by locals for access to crops or for hunting (Sousa 2008, Sousa et al. 2011).

Our estimates of chimpanzee densities for each habitat type show an inverse relationship with habitat availability (Figure 2), which highlights the preference for building nests and the suitable nesting conditions offered by dense-canopy forests. The present results confirm previous studies (Sousa 2008, Sousa 2009, Sousa et al. 2011) in demonstrating that tree canopy cover plays an important role in habitat choice for nest building in chimpanzees from Guinea-Bissau, in contrast to what has been found at other sites (Tutin and Fernandez 1984, Pruetz et al. 2002, Hernandez-Aguilar 2006, Boyer 2011). As an adaptation when dealing with declines of their preferred habitat, chimpanzees evidently opt to nest in savannah-woodlands (Tutin and Fernandez 1984, Marchesi et al. 1995). LCNP chimpanzees also use open canopy forests for nest building, which taken together underscores the importance of considering all habitat types for estimating chimpanzee densities, and also with respect to conservation efforts.

Method selection is a compromise between sound and well-established methodologies and the available resources and personnel (Marshall et al. 2008). Population size estimates of primates rely on certain assumptions, which vary depending on the different methodologies available (Whitesides et al. 1988, Kühl et al. 2008, Marshall et al. 2008, Boyko and Marshall 2010). Several studies applied nest count methods (Table S3). Nest production rates are usually taken from long-term monitoring of habituated chimpanzees due to the difficulty of observing wild chimpanzees (Plumptre and Reynolds 1997, Kühl et al. 2008). Despite the differences found

in this variable between sites and seasons, many studies used non-site specific information (see Table S3).

Our estimate of nest decay corresponds only to the dry season and with 293.9 days (%CV= 58.80) for 2010 was close to those reported from other locations within the western chimpanzee's range (Table S4). Further studies are required during the rainy season to compare robust estimates of the life span of nests from LCNP with those from other sites. Although we applied SCNC to estimate chimpanzee densities among habitats the overlap of the confidence intervals indicates low power to detect changes (Figure 2, Table 2). In future research we suggest that the decay rate presented here be incorporated when using SCNC. However, as decay rate depends on unmeasured covariates that may vary temporally and spatially (Buij et al. 2003, Kouakou et al. 2009), to avoid bias and obtain an accurate population size estimate, we recommend a new estimate under actual survey conditions (Marques et al. 2013) by monitoring the decay of new nests during successive visits.

Other techniques have emerged that deal with the time consuming process of monitoring the decay of a large and diverse sample of nests to obtain accurate estimates of life span of nests (Laing et al. 2003). For example, assuming a Markov chain for the state of a nest, with an absorbing state which represents nest disappearance, van Schaik et al. (1995) were able to estimate the time a nest takes to disappear based on the observation of nests (and their corresponding state) over time. For more details see (van Schaik et al. 1995, Buij et al. 2003, Kühl et al. 2008). Current work in progress based on our data set uses both state space models (D. L. Borchers, pers. comm.) and hidden Markov Models (R. Langrock, pers. comm.) to simultaneously estimate nest decay rate and abundance.

Chimpanzee distribution in relation to human disturbance

Even though chimpanzees reportedly show a certain ability to coexist with humans (Hockings 2007), places they consider safe for nest building have previously been shown to be distant from human settlements, roads, and rivers (Kuehl et al. 2009, Stokes et al. 2010, Vanthomme et al. 2013), further pointing towards a perhaps not surprising negative influence of human disturbance on chimpanzee distribution.

A recent meta-analysis by Junker et al. (2012) showed that measures of human impact such as proximity to settlements make a large contribution to the loss of suitable ecological conditions for chimpanzees. Historically most of the chimpanzee populations in Guinea-Bissau had human settlements within their range, and hence people regularly come into contact with chimpanzees on roads (main and secondary roads), in cultivated areas, and around the edges of forest fragments (Hockings and Sousa 2011).

Roads have been shown to be prejudicial for chimpanzee populations as they facilitate poaching and illegal hunting, and indirectly boost illegal logging (Hashimoto 1995, Devos et al. 2008), as has also been reported for other primates and other taxa such as ungulates, rodents and carnivores (Fa et al. 2002, Yackulic et al. 2011).

Cashew nuts are Guinea-Bissau's principal cash crop, representing 90% of the country's exports since 2000 (Baldé 2008, UNEP 2008). Most of the roads and settlements in LCNP are surrounded by extensive cashew plantations. Replacement of native forest by these monocultures reduces the availability of those trees that have canopies suitable for chimpanzees to build their nests. The cashew pulp is widely appreciated by many taxa, and some farmers reported that chimpanzees sometimes split branches while trying to reach the fruit at greater heights, leading to irreversible damages of trees and often resulting in chimpanzee-human conflict (S. Camará, pers. comm.). This study coincided with the period of cashew harvesting (March to late June), when the number of people inside the park, as well as road traffic, usually increases. Unlike the park residents, in general, these temporary harvest workers show little awareness with respect to the conservation of park biodiversity, compromising and undermining the conservation efforts by guards and residents.

The distributions of several forest-dwelling primate taxa in west and central Africa have been shown to be limited by rivers; larger rivers have a greater barrier effect on species distribution of forest taxa than smaller rivers, as observed for the Congo River and the rivers bounding the Dahomey Gap (Harcourt and Wood 2012). The Dahomey Gap, a dry savanna corridor interrupting the West African rainforest, has been a barrier for primate species either by its aridity or by its flanking rivers, the Volta and Niger (Harcourt and Wood 2012). The main rivers surrounding Lake Tumba, Congo, have also acted as a barrier, influencing the distribution of bonobos and chimpanzees (Inogwabini et al. 2012). LCNP is delimited by two main rivers, the Corubal in the north and the Buba River in the south, which limits the

chimpanzee distribution north and south of the protected area (Figure 1). People living in remote areas of LCNP with limited road access use navigable rivers as transportation routes, which could have the same negative impact on chimpanzees as roads.

Methodological implications

Chimpanzee populations worldwide are declining at alarming rates and an immediate reclassification of chimpanzees to a status of "critically endangered" has been recommended (e.g. (Walsh et al. 2003)). In light of such declines there is an urgent need to standardise appropriate designs and methodologies for long-term monitoring if the conservation of remaining chimpanzee populations is a priority for biodiversity management (Morgan et al. 2006). In this context, it is essential to consider the bias associated with a certain survey methodology, as well as its efficiency and cost-effectiveness (Ogutu et al. 2006). How can we reliably detect population declines within and between protected areas? What is the best way to provide baseline information for long-term population monitoring? In this regard it is crucial to stress that using trails or reconnaissance surveys might result in biased density estimates, compared to line transect surveys based on randomly placed transects, which, although more labour-intensive and expensive, should be the method of choice as they provide unbiased and potentially more accurate population estimates (Buckland et al. 2001). SCNC have been a viable and economical way to detect population declines, and procedures of monitoring programs and assessment of human impacts are performed using MNC surveys. The Ape Populations, Environments, and Surveys (A.P.E.S) Database aims to compile existing great ape survey data and make density and distribution data accessible to the scientific community (http://apes.eva.mpg.de). Our data will be made available in this database to help incentivize more standardized monitoring efforts and enable comparisons between different study sites (Campbell et al. 2008, Junker et al. 2012).

Final Considerations

Long-term population monitoring in LCNP, an important refuge for coastal populations of the western chimpanzee, would be highly desirable and may be achieved by investing in local training and capacity building. In general, human communities need to be included in conservation management, for instance by employing local people as park guards or tourist guides, to ensure effective long-term conservation (Kormos et al. 2003). As a mitigation

measure to minimize human-chimpanzee conflict it would be desirable to concentrate crops, including future cashew plantations, in zones that are already disturbed and where environmentally sustainable practices could be implemented (Vanthomme et al. 2013). We also recommend an effective control of illegal hunting by strengthening and enforcing the existing law, which forbids poaching (Decree No. 21/1980).

As ours, several other studies have shown the importance of protected areas for the preservation of stable primate populations. As there is evidence, however, that primates continue to use resources outside protected areas, recent studies advocate a landscape-scale conservation approach that takes into account the ecological requirements of species at larger spatial scales (Stokes et al. 2010, Jones 2011, Butsic et al. 2012).

Finally, our study contributes to our understanding of ecological patterns and how chimpanzees are influenced by human disturbance. In this regard it is, however, important to keep in mind that the chimpanzee-human relationship is complex, and present-day distribution patterns may not be explained alone by currently measurable variables as they may in part also reflect species adaptive responses to historical human activities.

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Supporting Material

Table S1. Deforestation rate in Guinea-Bissau based on Landsat satellite imagery from 1990 to 2007 [data from Oom et al. (2009)].

Habitat type	% per year	% of total area	% of area
Savannah-woodland	↑ 0.76	↑ 13	48
Mangroves	↑ 0.83	↑ 14	9
Open canopy forest	↓ 1.17	↓ 15	25
Dense canopy forest		↓ 50	3
Other	-	-	15

Table S2. Chimpanzee density estimates (builders/km^2) for each habitat and for the *Lagoas de Cufada* Natural Park obtained in 2010 based on marked-nest counts, using strip transect surveys.

Survey habitat	Density (builders/km^2)	95% CI[a] (builders/km^2)	%CV[b]
Global[c]	0.50*	0.18-1.39	52.90
Dense canopy forests	1.10*	0.00-2.42	72.21
Open canopy forests	1.09*	0.00-3.62	62.11
Savannah-woodlands	0.00	-	-

[a]Confidence interval.
[b]Coefficient of variation.
[c]Average nest density weighted by habitat.
*after defining strip transects (DF, *s*=6m; OF, *s*=16m; Sav, *s* =35m).

Table S3. Estimates of chimpanzee densities (chimpanzees/km^2) and population size reported for several study sites based on *nest count methods*. Estimates of chimpanzee densities from Guinea-Bissau are shown in italics.

Subspecies	Location	Study site	Estimates of density	Population size	Data source
P. t. verus	Guinea-Bissau	Cantanhez NP	*1.94-2.34*	33-40	Sousa (2007)
		Gadamel	*0.90*	33	Sousa (2009)
		Lagoas de Cufada Natural Park	*0.75 (0.27-1.67)*	281	Sousa (2008)
			0.22 (0.08-0.62)	137	This study (2011 survey)
	Guinea	Nationwide	N/A	1,420-6,625*	Sugiyama and Soumah (1988)
		Haut Niger NP	0.87	N/A	Fleury-Brugiere and Brugiere (2010)
		Koulako	1.09	N/A	
		Moyeria	0.90	N/A	Ham 1998 *in* Ganas (2009)
		Siria	0.26	N/A	
		Diecke Forest	0.17	N/A	
	Ivory Coast	Taï NP	0.09-1.7	11,676±1,168	Marchesi et al. (1995)
			2.19 (core area)	105	Kouakou et al. (2009)
			0.15 (periphery)	7	
	Liberia	Sapo Forest	0.24 (0.18-0.77)	240	Anderson et al. (1983)
	Mali	Bafing Forest Reserve	0.27	N/A	Pavy 1993 *in* Fleury-Brugiere and Brugiere (2010)
		Faragama	0.30	N/A	Granier and Martinez 2004 *in* Fleury-Brugiere and Brugiere (2010)
		Djakoli	0.39	N/A	
	Senegal	Niokolo Koba NP (Mt. Assirik)	0.13	N/A	Pruetz et al. (2002)
		Fongoli	0.09	N/A	
		Kharakhena	0.08-0.19	34	Boyer (2011)
		Koudekouru (Bofeto)	0.04-0.09	34	
	Sierra Leone	Gola Forest Reserves	0.27 (0.18-0.41)	305 (203-458)	Ganas (2009)
P. t. troglodytes	Camaroon	Dja Reserve	0.79 (0.60-1.04)	N/A	Williamson and Usango 1996 i*n* Morgan et al. (2006)
	Central Africa	Nationwide	0.01-0.13	N/A	Carroll 1986 *in* Blom et al. (2001)
		Dzanga-Ndoki NP	0.16	79	Blom et al. (2001)

	Congo	Lac Télé Community Reserve	0.70 (0.4-1.3)	N/A	Poulsen and Clark (2004)
		Goualougo Triangle	1.53 (1.21-1.93)		Morgan et al. (2006)
	Equatorial Guinea	Rio Muni	0.31-1.53	N/A	Jones and Sabater Pi 1971 *in* Morgan et al. (2006)
	Gabon	Belinga	0.32 (0.03-0.49)	64,173±13,000	Tutin and Fernandez (1984)
		Petit Loango Reserve	0.78	N/A	Furuichi et al. (1997)
P. t. schweinfurthi	Congo	Kahuzi-Biega	0.40	7,670 (4,180-10,830)	
		Kasese	0.11	3,350 (1,420-5,950)	Hall et al. (1998)
		Odzala NP	2.20	N/A	Bermejo (1999)
	Tanzania	Malagarasi River to Karema	0.21*	N/A	Kano 1972 *in* Hashimoto (1995)
		Kwitanga Forest	0.69 (0.31-1.54)	15 (7-34)	Ndimuligo (2007)
	Uganda	Kalinzu Forest	2.8 - 4.7	384-644	Hashimoto (1995)
		Kibale Forest	1.97	1509	Ghiglieri (1984)
		Budongo Forest	1.3 - 2.5	570-1066	Plumptre and Reynolds (1996)

*results based on questionnaires
NP- National Park
N/A- Not Available

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Table S4. Life span of nests from several study sites, including our estimate of nest decay for *Lagoas de Cufada* Natural Park.

Subspecies	Location	Study site	Mean nest life span (days)	Season	Data source
P. t. verus	Guinea-Bissau	*Lagoas de Cufada* Natural Park	293.9	dry	This study (2010 survey)
	Guinea	Haut Niger	221.0	both	Sugiyama and Soumah (1988)
	Ivory Coast	Taï NP	194.0	both	Fleury-Brugiere and Brugiere (2010)
			91.2	both	Kouakou et al. (2009)
			73.3	both	Marchesi et al. (1995)
P. t. troglodytes	Gabon	Belinga	113.6	both	Tutin and Fernandez (1984)
		Northeastern Gabon	112.8	N/A	Tutin and Fernandez 1981 *in* Anderson et al. (1983)
	Central Africa	Dzanga-Ndoki NP	50.9	both	Blom et al. (2001)
	Congo	Goualougo Triangle	90.0 or 91.5?	both	Morgan et al. (2006)
	Gabon	Lope	106.0	both	White, unpublished *in* Hall et al. (1998)
P. t. schweinfurthi	Tanzania	Mahale Mountains NP	131.0	both	Ihobe (2005)
	Uganda	Gombe NP	36.0	N/A	Moyer et al. (2006)
		Ugalla Forest	97.0	N/A	Plumptre and Reynolds (1996)
		Budongo Forest	37.2	dry	
			54.6	Wet	
			45.9	both	
		Kibale	111.0	N/A	Ghiglieri (1979)

NP- National Park
N/A- Not Available

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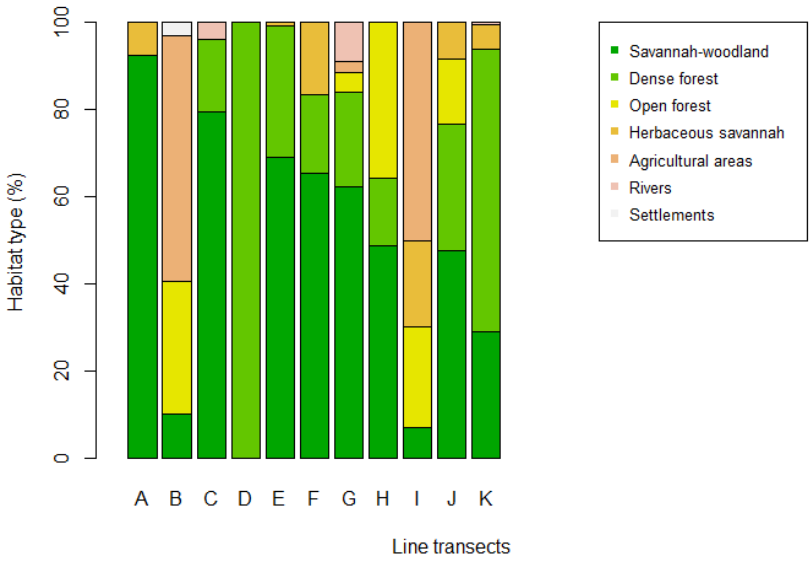

Figure S1. Relative proportions of habitat type found along each line transect.

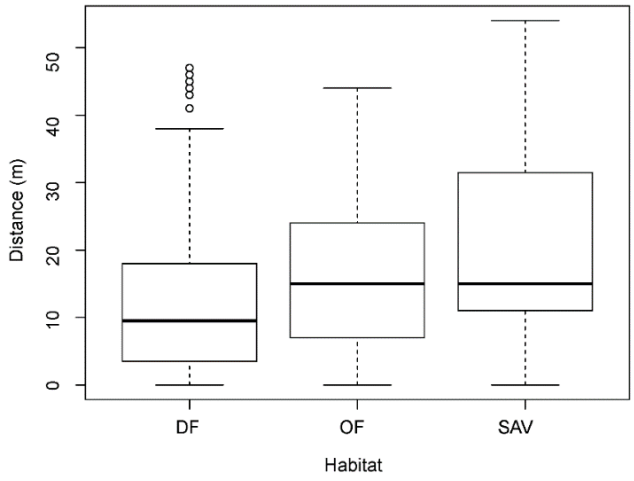

Figure S2. Boxplots showing the distances at which nests were detected from the line transects. The data from 2010 and 2011 surveys were combined, and distances truncated at >60m.

Chapter 3

Chimpanzee Nesting Patterns

Resumo

Várias populações de chimpanzé encontram-se distribuídas em fragmentos florestais intercalados com comunidades humanas, estando sujeitas a uma constante alteração da estrutura e composição das áreas florestadas adequadas à sua sobrevivência. Deste modo, é necessário determinar-se as características da vegetação associadas à abundância e distribuição dos chimpanzés nestas paisagens antropogénicas, porém poucos estudos investigaram quantitamente esta relação. O método de contagem individual de ninhos foi aplicado ao longo de 11 transectos lineares sistematicamente distribuídos no Parque Natural das Lagoas de Cufada (PNLC), durante a estação seca de 2010 e 2011. Este parque representa uma das sete áreas listadas na Rede Nacional das Áreas Protegidas da Guiné-Bissau e é caracterizado por um mosaico de floresta-savana bastante perturbado por actividades humanas. Para cada ninho de chimpanzé, *Pan troglodytes verus*, recolheu-se informação sobre o tipo de habitat, a espécie de árvore que alberga o ninho e a altura de construção. Diferentes tipos de habitats foram descritos ao longo dos transectos lineares (plantas com diâmetro à altura do peito > 10 cm; 2,5 m para cada lado). Primeiro, investigou-se o efeito de características da vegetação - riqueza, diversidade e composição florística, densidade e área basal das árvores - na abundância de ninhos de chimpanzés. Segundo, a distribuição das alturas de construção de ninhos foi avaliada para determinar suporte para a estratégia de anti-predação, isto é em locais onde a abundância de predadores (p.e. leopardos) é elevada os chimpanzés constroem ninhos a alturas maiores do que em locais onde a pressão é baixa ou ausente. Por último, avaliou-se o padrão de selecção de espécies de árvores para construção de ninhos relativamente a outras populações de *P. t. verus*. Atendendo à elevada frequência de zeros normalmente observada em estudos ecológicos, modelos inflacionados de zeros foram usados. Com base num modelo binomial negativo inflacionado em zero com efeito aleatório, a abundância de ninhos surgiu negativamente associada à diversidade florística (avaliada pela forma exponencial do índice de Shanon) e positivamente à disponibilidade de árvores baixas, reflectindo características da floresta de canópia densa. Por outro lado, a correlação positiva obtida entre a abundância de ninhos e a riqueza (i.e. o número de espécies de plantas) e composição florística sugere que quer a floresta de canópia esparsa quer a

savana arborizada são habitats também importantes na construção de ninhos. A maioria dos ninhos (90%) foi construída em espécies incluídas na dieta dos chimpanzés, surgindo também positivamente associada à disponibilidade de árvores baixas., característica da vegetação da floresta densa. De acordo com outros estudos, os chimpanzés foram selectivos na escolha das espécies de árvores para construção de ninhos, mas em contraste com outras populações de *P. t. verus* não demonstraram preferência pela construção de ninhos em palmeira-de-óleo (*Elaeis guineensis*). A construção exclusiva de ninhos em árvores no PNLC sugere ser uma consequência da pressão humana, porém futuros estudos são necessários para se averiguar até que ponto a construção de ninhos a alturas elevadas compreende uma resposta a predadores capazes de subir às árvores. Sendo o PNLC um importante refúgio no limite Ocidental de distribuição geográfica de *P. t. verus*, porém bastante ameçado pela pressão humana, é necessário definir estratégias de conservação para os habitats adequados à sobrevivência dos chimpanzés nesta área protegida.

Palavras-chave: características da vegetação; chimpanzé; construção de ninhos; estratégia de anti-predação; Guiné-Bissau; uso de habitat.

Paper II. Where to nest? Ecological determinants of chimpanzee nest abundance and distribution at the habitat and tree species scale

Carvalho J. S., Meyer C. F. J., Vicente L., and Marques T. A. 2014. *Am. J. Primatol.* In press.

Abstract - Conversion of forests to anthropogenic land-uses increasingly subjects chimpanzee populations to habitat changes and concomitant alterations in the plant resources available to them for nesting and feeding. Based on nest count surveys conducted during the dry season, we investigated nest tree species selection and the effect of vegetation attributes on nest abundance of the western chimpanzee, *Pan troglodytes verus*, at Lagoas de Cufada Natural Park (LCNP), Guinea-Bissau, a forest-savannah mosaic widely disturbed by humans. Further, we assessed patterns of nest height distribution to determine support for the anti-predator hypothesis. A zero-altered generalized linear mixed model showed that nest abundance was negatively related to floristic diversity (exponential form of the Shannon index) and positively with the availability of smaller-sized trees, reflecting characteristics of dense-canopy forest. A positive correlation between nest abundance and floristic richness (number of plant species) and composition indicated that species-rich open habitats are also important in nest site selection. Restricting this analysis to feeding trees, nest abundance was again positively associated with the availability of smaller-sized trees, further supporting the preference for nesting in food tree species from dense forest. Nest tree species selection was non-random, and oil palms were used at a much lower proportion (10%) than previously reported from other study sites in forest-savannah mosaics. While this study suggests that human disturbance may underlie the exclusive arboreal nesting at LCNP, better quantitative data are needed to determine to what extent the construction of elevated nests is in fact a response to predators able to climb trees. Given the importance of LCNP as refuge for *P. t. verus* our findings can improve conservation decisions for the management of this important umbrella species as well as its remaining suitable habitats.

Key-words: Guinea-Bissau; hurdle models; nest tree species selection; nesting patterns; vegetation attributes; western chimpanzee.

3.1 Introduction

Over large geographic scales distribution patterns of primates are shaped by historical biogeography and environmental constraints (Lehman and Fleagle 2006, Kamilar 2009), and communities living in close geographic proximity and under the same environmental conditions should exhibit similar species composition (Lehman 2006, Kamilar 2009). The distribution of primates can additionally be influenced by human disturbance along a gradient of geographic scales (Rovero and Struhsaker 2007, Potts 2011).

At small spatial scales, primate distribution is determined by topographical features and vegetation attributes (Furuichi and Hashimoto 2004, Ndimuligo 2007). Vegetation attributes such as floristic richness, diversity and composition, tree size and density, and fruit abundance, are commonly used predictor variables in studies assessing correlates of primate abundance (Furuichi and Hashimoto 2004, Wieczkowski 2004, Cristóbal-Azkarate et al. 2005, Rovero and Struhsaker 2007, Stevenson 2011, Linder and Lawler 2012). These attributes also reflect the distribution of the tree species preferentially selected for nesting and feeding (Furuichi and Hashimoto 2004, Ogawa et al. 2007). Most of these studies have contributed significant information regarding patterns of habitat preference, but few have quantitatively assessed vegetation correlates of primate abundance and distribution (Hanya and Chapman 2013), including for chimpanzees (Balcomb et al. 2000, Hernandez-Aguilar 2006).

Most mammals spend a large time of their lives sleeping or resting in building burrows, caves, dens, nests, or other shelters (Eisenberg 1983), which provide protection from environmental challenges (Stewart et al. 2011). We use the term "nest" throughout the paper when referring to the sleeping platforms constructed by chimpanzees, although they differ fundamentally from those of other nest-building animals in terms of their function (see Samson and Hunt 2012). Since great apes, in contrast to all other nonhuman primates (Anderson 2000), build a nest every night for sleeping or resting during the day, nest abundance has been a useful surrogate for estimating densities and population sizes as well as for assessing their home range (Fruth and Hohmann 1996, Buij et al. 2003, Devos et al. 2008, Carvalho et al. 2013). Nest site distribution may also inform about the distribution of food resources (Furuichi and Hashimoto 2004).

Although for some study sites it has been documented that chimpanzees build their nests on the ground (Furuichi and Hashimoto 2000, Hicks 2010, Koops et al. 2012b, Last and Muh 2013), arboreal nest building is most frequent and its function has been explained through the following non-mutually exclusive hypotheses: antipredation (Baldwin et al. 1981, McGrew 2004, Pruetz et al. 2008, Hernandez-Aguilar et al. 2013), antipathogen (Fruth and Hohmann 1996, Anderson 1998), thermoregulation (McGrew 2004, Koops et al. 2012a, Samson and Hunt 2012), and promotion of mental health (Fruth and Hohmann 1996, Anderson 1998). In this context, many studies suggest that nest height and canopy cover, among other variables, are important determinants of arboreal nesting patterns, in line with the predation avoidance hypothesis (Goodall 1962, Baldwin et al. 1981, Pruetz et al. 2008).

Several studies have documented that chimpanzees only use a subset of the total floristic richness available at a site for nest building and, among those tree species used, only select a few in greater proportions (Furuichi and Hashimoto 2004, Ndimuligo 2007, Stanford and O'Malley 2008, Koops et al. 2012a). Nest tree species selection is not an exclusive behaviour of chimpanzees, and has also been reported for other great apes (Fruth and Hohmann 1996, Rothman et al. 2006, Cheyne et al. 2013). Whereas some studies have reported a preference of the western chimpanzee, *Pan troglodytes verus*, for nesting in oil palms (Barnett et al. 1996, Sousa et al. 2011), others found no such evidence (Seringbara (Guinea), Humle and Matsuzawa 2004), and the underlying causes for such preference remain generally understudied, highlighting the need for more data across the species geographic distribution range to understand this preference.

Pan t. verus has been classified as Endangered on the IUCN Red List since 1988 (IUCN 2014) and has suffered a loss of 11% in the area of suitable environmental conditions since 1986 (Torres et al. 2010, Junker et al. 2012), anthropogenic causes being the main driver of this decline. In this paper, we provide a quantitative assessment of vegetation correlates of western chimpanzee nest abundance in a protected but highly human-modified landscape in Guinea-Bissau. We also assess patterns of nest height distribution to evaluate the anti-predation hypothesis. Finally, we investigate patterns of nest tree species selection to further our understanding of how this behavior varies geographically across the species' range. Understanding cultural, environmental and ecological factors that shape distribution patterns of *P. t. verus* at small geographic scales will improve future management strategies to ensure its long-term conservation at the westernmost margin of its geographic distribution.

3.2 Methods

Study Site

The study was conducted in Lagoas de Cufada Natural Park (LCNP, between 11º34' and 11º51' N and 14º49' and 15º16'W), a protected area in Guinea-Bissau that covers 890 km^2 (IBAP 2008) (Fig. 1). Its climate is characterized by an average temperature of about 26ºC during both the dry and rainy season. Annual rainfall averages 2200 mm, which mostly falls in the rainy season between June and October, with almost no precipitation (<100 mm) in the pronounced dry season between November and May (Catarino et al. 2002; http://sdwebx.worldbank.org/climateportal/index.cfm, IBAP 2008). LCNP is a Ramsar Convention site characterized by an extensive network of rivers, streams, and lagoons whose water levels fluctuate strongly depending on rainfall, with some rivers and streams drying up towards the end of the dry season (IBAP 2008). The park topography is relatively flat, reaching a maximum of 39 m of altitude, and soil composition and its depth varies, which defines and limits the presence of plant species (Catarino et al. 2006a).

LCNP is characterized by a mosaic of different habitats at different stages of degradation and early regeneration as a consequence of human disturbance (Catarino et al. 2006a). The habitat types suitable for chimpanzee nest building are dense and open canopy forests, and savannah-woodland. Other habitats such as herbaceous savannah, swamp forest and mangrove have no suitable trees for nesting. Dense-canopy forest is structurally and compositionally similar to the multi-storeyed forests of Sierra Leone and Liberia (FAO 1995). This forest type is characterized by high canopy coverage (ca. 90%) and a typically poorly developed understory. The most common species are *Afzelia africana*, *Albizia* spp., *Antiaris toxicaria*, *Ceiba pentandra*, *Chlorophora* spp., *Detarium senegalense*, *Dialium guineense*, *Elaeis guineensis*, *Erythrophleum guineense*, *Malacantha alnifolia*, *Parkia biglobosa*, *Parinari excelsa*, and *Spondias mombin* (FAO 1995, Catarino et al. 2006b). Open-canopy forest (60-70% canopy cover) is dominated by *Borassus aethiopium*, *Daniellia oliveri*, *P. biglobosa*, and *Piliostigma thonningii*. Open forest and savannah-woodland have some tree species in common, due to their occurrence on similar soil types (Catarino et al. 2006a). Other tree species are, however, restricted to savannah-woodland (about 20-40% canopy cover): *Albizia zygia*, *Crossopteryx febrifuga*, *Lophyra lanceolata*, *P. thonningii*, *Pterocarpus erinaceus*, *Terminalia albida*, as well as some species of *Combretum* and *Ficus*. For more details see Catarino et al. (2006a, b).

The relative proportions of these habitat types in LCNP (dense forest: 9%, open forest: 35%, savannah-woodland: 54%; (Amaro 2011)) roughly correspond to their total occurrence countrywide (dense forest: 3%, open forest: 25%, savannah-woodland: 48%; (Oom et al. 2009)).

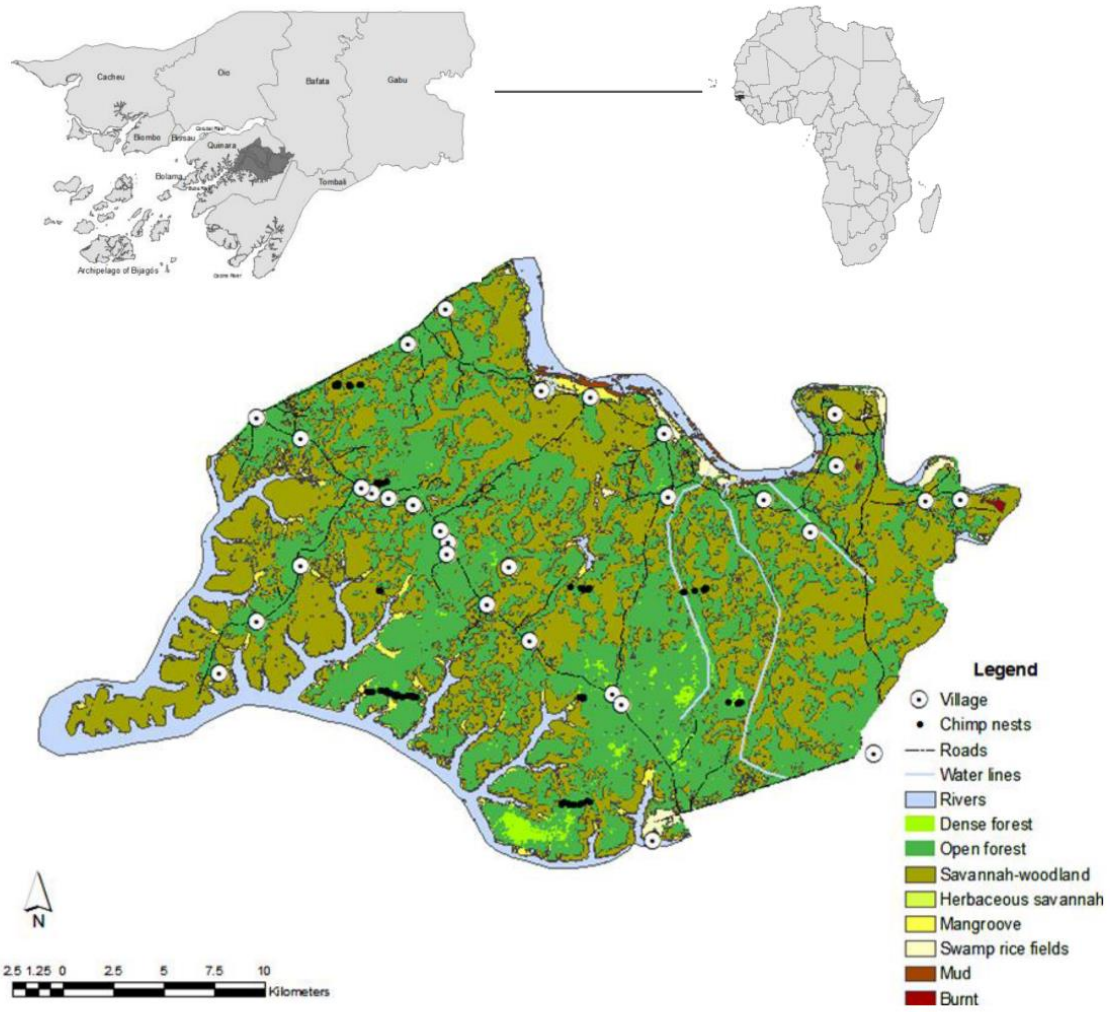

Figure 1. Location of the Republic of Guinea-Bissau in West Africa and the study area *Lagoas de Cufada* Natural Park (LCNP). Nest locations along the transects sampled inside LCNP are shown. Environmental digital data were provided by the CARBOVEG project (http://carboveg-gb.dpp.pt/).

Chimpanzee Nest Surveys

This research adhered to the American Society of Primatologists (ASP) principles for the ethical treatment of primates as well as to the legal requirements of the governmental agency that manages the protected areas in Guinea-Bissau (*Instituto da Biodiversidade e das Áreas Protegidas*).

Due to the difficulty of observing chimpanzees themselves nests were recorded as indirect evidence of their presence. The sampling design was initially defined for an application of line transect distance sampling, with repeated visits to eleven systematically placed linear transects to estimate chimpanzee densities (Carvalho et al. 2013). Transects were walked at a steady speed of about 1 km /h and all nests visible from the transect line were recorded, using binoculars when necessary. Nest counts were conducted during the dry seasons of 2010 and 2011 (4 visits between February and April 2010 and 5 visits between February and May 2011, in biweekly sampling intervals). Total survey effort comprised 302.4 km. Nest trees were tagged with a rope to avoid double counting and the number of nests encountered during each visit was recorded. However, as we did not record nest position and also have no information on the reuse of old nests, nest counts may constitute slight underestimates. For the purpose of this study, we pooled nests of all ages. For each nest, the habitat type in which it was observed, tree species, and nest height (measured from the ground to the base of the nest by using a laser range finder, Bushnell Yardage Pro Sport 450) were recorded.

Habitat Description

A qualitative and quantitative assessment of the vegetation was conducted from October to December 2009 along 5 linear transects randomly chosen from among the 11 used during nest surveys (2.5 m to each side, approximately 3 km in length, 15.2 km total survey effort). Habitat boundaries were geo-referenced to determine the proportion of each habitat along these transects. Each transect comprised a variable number of units of habitat types (hereafter referred to as sampling units, SU). All plant species >10 cm diameter at breast height (dbh, measured at a height of 1.5 m) were identified and counted, and the corresponding dbh measured using a tape measure. Where two trunks originated from the same base each was measured independently and the average of these was taken as the overall measurement for that tree. Plant species identification was done with the help of the park guards and other

locals. When necessary, samples were collected for later identification at the herbarium of the *Instituto de Investigação Científica e Tropical* (Lisboa, Portugal).

Data Analysis

All analyses were conducted in R version 3.0.2 (R Development Core Team 2013). Reported values are mean ±1SE unless otherwise noted**.**

To test for a habitat effect on nest height a generalized linear mixed model (GLMM) was performed using the package *lme4* (Bates et al. 2012), using a Gaussian distribution and identity link function and including tree species as a random factor.

Vegetation attributes - floristic richness, diversity and composition, plant density (plant abundance /0.1 ha), and total basal area (m^2 /0.1 ha) - were calculated for each SU, considering only native species (i.e. agricultural species were excluded). Because the SUs differed in size and number of species, we standardized the data by (1) converting abundances into relative densities, i.e. the abundance of each species was standardized to 0.1 ha and weighted by the total density obtained for each SU, and by (2) using sample-based rarefaction to calculate the number of species expected in a subset of individuals selected at random from a larger sample (Gotelli and Colwell 2010). Sample-based rarefaction was computed using EstimateS software (Colwell 2013). Comparisons of rarefied species richness among habitats were made at 5 samples, the maximum number of SUs in common across habitat types. Vegetation attributes were calculated based on the relative density of native species in 18 SUs of 0.1 ha, considering either the entire floristic assemblage (N=93 species) or only plant species known to be consumed by LCNP chimpanzees during the dry season (N=22 species; see Table SI). The floristic diversity of each SU was measured using the exponential form of the commonly used Shannon entropy index (e^H) (Jost 2006). To assess statistical differences among SUs in plant density and diversity, and total basal area, the non-parametric Kruskal-Wallis test was employed. Linear regression was used to test for a correlation between average nest height and mean dbh of tree species used for nesting (using dbh data from the vegetation surveys as a proxy for nest tree dbh).

To compare community-level patterns of floristic composition across habitats non-metric multidimensional scaling (NMDS) was used. NMDS is a robust, non-linear ordination

technique considered an efficient method to analyse ecological community data (McCune and Grace 2002). The goodness of fit of the final ordination is evaluated by the stress, a measure of how good the *m*-dimensional configuration is (see Zuur et al. 2007). Statistical significance of the variation of floristic composition among habitats was investigated with a permutational multivariate ANOVA (PERMANOVA), which consists in assessing differences between *a priori*-defined groups of community samples based on a (dis)similarity matrix (Clarke 1993). To interpret the ordination, plant species and total basal area were added to the plot using vector fitting, i.e. plotting arrows that represent the direction of the variables gradient and the correlation between ordination axes and these variables (Oksanen et al. 2012). For plotting, the axes were scaled by the square root of the square correlation coefficient (R^2) and P-values were computed based on 999 permutations. NMDS and PERMANOVA were performed using the package *vegan* (Oksanen et al. 2012), based on a Bray-Curtis distance matrix.

Appropriate statistical approaches to deal with the high frequency of zeroes often found in ecological count data should be applied as these can influence the predictive performance of models and ecological inference (Martin et al. 2005, Linder and Lawler 2012). In ecological data two types of zero counts are often encountered: true zeroes, when a species or indirect signs of its presence are absent from the survey area, and false zeroes, when an animal or indirect evidences are present but the observer failed to record them (see Zuur et al. 2009). We accounted for the presence of excess zeroes by fitting zero-inflated (ZI) models and hurdle or zero-altered (ZA) models (Zuur et al. 2012) to the nest abundance data. ZI and ZA models have one important distinction in how they interpret and analyze zero counts (Zamani and Ismail 2013). A ZI model, also known as a mixture model, does not "know the truth" about a zero being false or true, and distinguishes two different origins for the probability of zero observations: coming from a count process and from a binomial (in fact strictly Bernoulli, i.e. binary) process (Zuur et al. 2009). On the other hand, a ZA model is a modified count model explicitly composed of two parts: one generating the positive values (i.e. non-zeroes), usually a truncated-at-zero count model, and one generating the zeroes, a binary response model (Cameron and Trivedi 1998).

We modelled nest abundance as a function of the aforementioned vegetation attributes (floristic richness, diversity and composition, plant density and total basal area) in a GLMM framework, specifying transects and visits to transects as random factors, and the area of each

SU and previous estimates of habitat-specific nest detectability (Carvalho et al. 2013) as an offset. For ZI models, a Poisson distribution or negative binomial distribution was used for nest count data, and a binomial distribution with a logit link for presence/absence data (Martin et al. 2005, Zuur et al. 2009). For ZA models, a Poisson distribution or negative binomial distribution was used to model the non-zero counts, and a binomial distribution with a logit link for fitting zeroes (Martin et al. 2005, Zuur et al. 2009). Collinearity among the explanatory variables was not severe: the maximum variance inflation factor (VIF) obtained was smaller (4.81) than the rule of thumb for the cut-off value (5) suggested by Neter et al. (2004). The small sample size version of Akaike's Information Criterion (AICc) was used for model selection (Burnham and Anderson 2002). We present only the parameter estimates and model diagnostics for the most parsimonious model. The analyses were performed using the R packages *glmmADMB* (Fournier et al. 2012, Skaug et al. 2012) and *MuMIn* (Bartón 2013).

To determine whether chimpanzee tree species choice for nesting deviates significantly from random we implemented a randomization test in R. We compared samples of tree species randomly selected from those available (random trees: RT) with those actually used for nest building (nest trees: NT, N=459). RT samples (N=459 trees, corresponding to the NT sample size) were selected by random sampling with replacement from the tree abundance data (N=1,963 trees, including 10 individuals of unidentified tree species). This procedure was repeated 1000 times to evaluate how far from the expected proportion at random (p_{RT}) each observed proportion was (p_{NT}). Thus, for each tree species, we obtained the distribution of the proportion of use if that species were chosen at random (p_{RT}). Plotting the expected p_{RT} distribution as a function of observed p_{NT} allows one to easily distinguish preferred tree species ($p_{NT}>p_{RT}$) from those avoided ($p_{NT}<p_{RT}$), depending on whether the distribution lies entirely below or above the 1:1 line, respectively. If the randomization distribution p_{RT} overlaps the 1:1 line this indicates that the observed p_{NT} might be observed as a result of random choice.

3.3 Results

Chimpanzee Nest Surveys

Only arboreal nests were found and mostly in dense forest (N=239), whereas fewer nests were observed in the two habitats with less canopy coverage: open forest (N=114) and

savannah-woodland (N=106) (see Carvalho et al. 2013). Most of the nests were built in tree species belonging to the two legume subfamilies Caesalpinioideae and Mimosoideae, and Palmae. Of the 23 tree species recorded with chimpanzee nests (Table I), at least 12 provide fruits eaten by LCNP chimpanzees during the dry season (Table SI) and 90% of the nests were built in those species.

Table I. Relative Proportion, Total Number, and Mean Nest Height (± SE) of Chimpanzee Nests Observed in 23 Tree Species, Along With the Corresponding Tree Family.

Tree species (abbreviation)	Family	Nests observed (%)	Nests (total)	Nest height (m)
Dialium guineense (D.guin)	Legum./Caesalp.	52.72	242	13.10 (0.02)
Elaeis guineensis (E.guin)	Palmae	10.02	46	19.93 (0.08)
Detarium senegalense (D.sene)	Legum./Caesalp.	5.66	26	17.66 (0.20)
Afzelia africana (A.afri)	Legum./Caesalp.	4.58	21	15.78 (0.17)
Parkia biglobosa (P.bigl)	Legum./Mimos.	4.36	20	16.34 (0.21)
Parinari excelsa (P.exce)	Chrysobalanaceae	3.70	17	15.15 (0.26)
Daniellia oliveri (D.oliv)	Legum./Caesalp.	3.49	16	14.50 (0.24)
Unidentified 39 (unid.39)	-	3.49	16	9.15 (0.22)
Pterocarpus erinaceus (P.erin)	Legum./Papil.	2.18	10	13.34 (0.28)
Khaya senegalensis (K.sene)	Meliaceae	1.96	9	16.76 (0.52)
Ceiba pentandra (C.pent)	Bombacaceae	1.31	6	21.25 (0.37)
Unidentified 41 (unid41)	-	1.31	6	21.23 (0.76)
Erythrophleum suaveolens (E.suav)	Legum./Caesalp.	1.09	5	14.65 (0.79)
Antiaris toxicaria subsp. welwitschii (A.toxi)	Moraceae	0.87	4	21.98 (0.82)
Newbouldia laevis (N.laev)	Bignoniaceae	0.65	3	15.33 (2.54)
Terminalia macroptera (T.macr)	Combretaceae	0.65	3	13.98 (0.38)
Cola cordifolia (C.cord)	Sterculiaceae	0.44	2	11.15 (0.35)
Spondias mombin (S.momb)	Anacardiaceae	0.44	2	12.65 (0.00)
Acacia macrostachya (A.macr)	Legum./Mimos.	0.22	1	4.65
Allophylus africanus (Al.afri)	Sapindaceae	0.22	1	11.65
Unidentified 5 (unid5)	-	0.22	1	7.65
Unidentified 22 (unid22)	-	0.22	1	13.65
Unidentified 40 (unid40)	-	0.22	1	16.75

Tree (sub) family: Legum. – Leguminosae; Caesalp. – Caesalpinioideae; Mimos. – Mimosoideae; Papil. – Papilionoideae.

Nest height averaged 14.60 ± 0.01 m across the full range of observed nest tree species (N=459), and 14.01 ± 0.01 m when excluding nests in oil palms (N=413), which due to their physiognomic distinctiveness often harbored nests higher on the trunk compared to other tree species (Table I). The greatest mean nest height was observed in savannah-woodland (16.71 ± 0.04 m), followed by dense forest (14.11 ± 0.02 m) and open forest (13.66 ± 0.05 m), however, differences were not significant (GLMM: $\chi^2 =$ 3.00, df=2, P=0.22) (Fig. 2). A positive correlation was found between average nest height and mean dbh of tree species used for nesting based on the vegetation surveys (R^2=0.27, F=7.232, P<0.05), although this relationship had low explanatory power (Table I; Table SI).

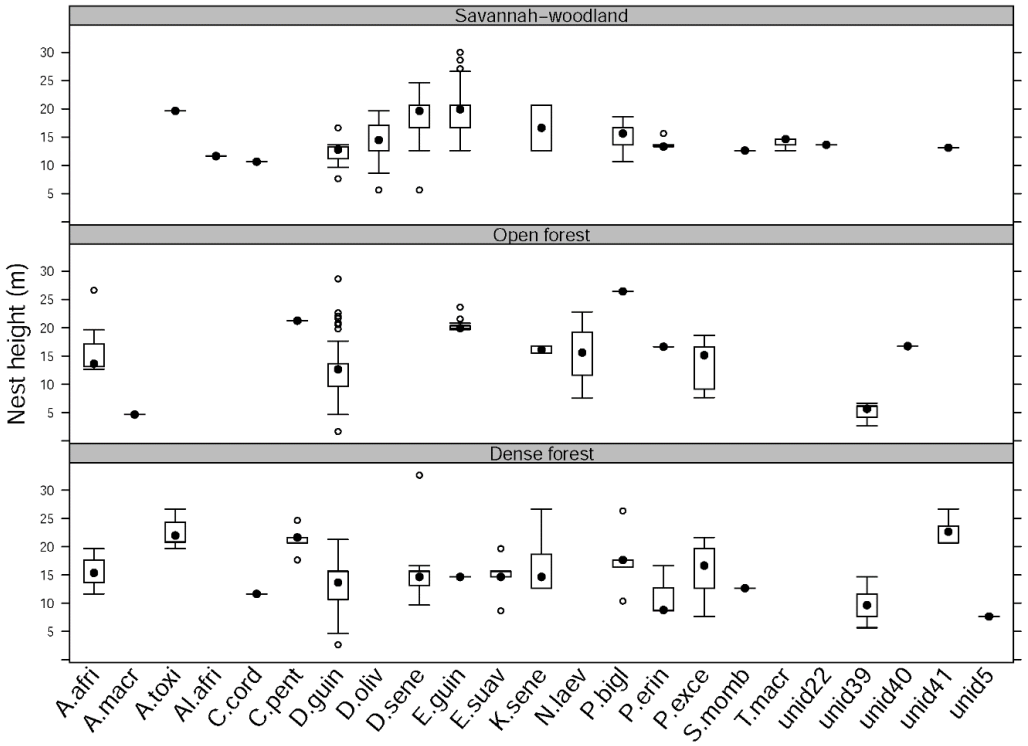

Figure 2. Boxplots comparing nest height among nest tree species and habitat types. See Table I for species names and abbreviations.

Habitat Description

A total of 2,005 individual plants were recorded, belonging to 85 tree (N=1,966) and 8 liana species (N=39) (Table SI). Datasets standardized by sample-based rarefaction confirmed that savannah-woodland was significantly more species-rich than either forest type, which showed similar levels of species richness (Fig. S1).

The two-dimensional NMDS ordination clearly separated savannah-woodland from open and dense forest plant communities along axis 1 which were more similar in floristic composition as indicated by the fairly tight clustering of SUs compared with the more heterogeneous floristic composition of savannah-woodland which showed considerable spread along axis 2 (Fig. 3; Table SII). PERMANOVA confirmed significant compositional variation among habitat types (R^2=0.25, F=2.455, P<0.001). The nest trees *D. guineense*, *E. guineensis* and *A. africana* showed a positive association with dense and open forests along axis 1, and *D. senegalense* and *P. biglobosa* were the nest trees associated negatively and positively, respectively, with savannah-woodland along axis 2 (Fig. 3). For more details see Supporting Material (Fig. S2).

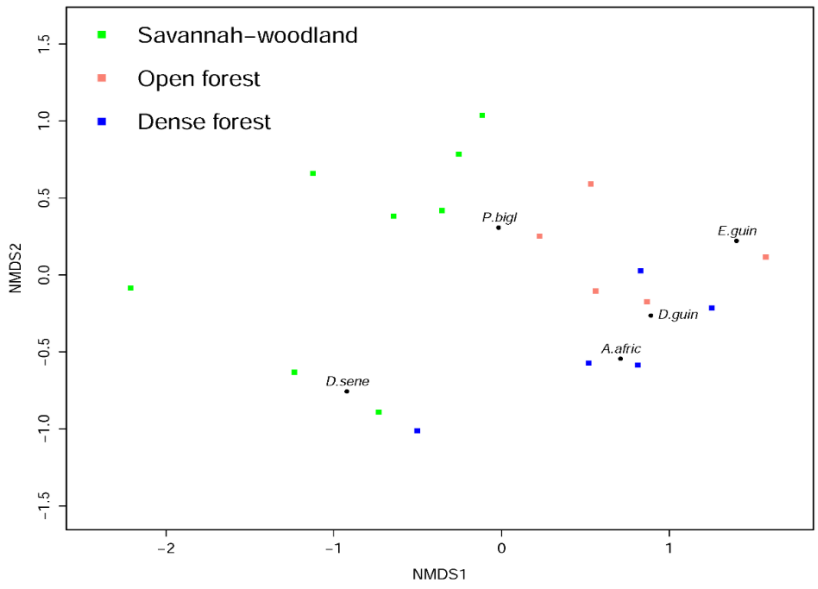

Figure 3. Ordination of sampling units along non-metric multidimensional scaling axes for the entire native floristic assemblage (stress=0.11). Also shown are five of the six tree species preferred for nesting (unidentified species 39 was not recorded during vegetation surveys). Tree species: see Table I.

Considering only plant species known to be eaten by LCNP chimpanzees, the same patterns were found for floristic richness, diversity and composition, as for the whole assemblage. For more details see Supporting Material (Fig. S3; Table SI and Table SII).

TABLE II. Results of AICc-Based Model Selection of GLMM Zero-Altered Negative Binomial Regression (ZANB) Models for the Effects of Vegetation Attributes on Chimpanzee Nest Abundance. Note that Results are Reported Considering Both the Entire Floristic Assemblage and Only Plant Species Known to be Eaten by LCNP Chimpanzees (see Table SI).

Sample	Parameter type	Variables	AICc	Δ AICc*
Entire floristic assemblage	Nest counts	FR, e^H, NMDS1, NMDS2, BA	168.87	0.00
		Full model	174.71	5.84
		FR, PD, e^H, NMDS1, NMDS2	174.73	5.86
		FR, PD, e^H, NMDS1, BA	180.27	11.40
		FR, PD, e^H, NMDS2, BA	181.88	13.01
		PD, e^H, NMDS1, NMDS2, BA	184.21	15.34
		FR, PD, NMDS1, NMDS2, BA	185.63	16.76
	Zeroes	PD, e^H, NMDS1, BA	138.61	0.00
		FR, PD, e^H, NMDS1, NMDS2	141.89	3.28
		FR, PD, e^H, NMDS1, BA	142.35	3.74
		PD, e^H, NMDS1, NMDS2, BA	142.80	4.19
		FR, PD, e^H, NMDS2, BA	143.79	5.18
		Full model	144.13	5.52
		FR, e^H, NMDS1, NMDS2, BA	144.35	5.74
		FR, PD, NMDS1, NMDS2,BA	145.48	6.87
Food plant species	Nest counts	BA	166.73	0.00
		FR, e^H, NMDS1, NMDS2, BA	182.27	15.54
		FR, PD, NMDS1, NMDS2, BA	182.27	15.54
		FR, PD, e^H, NMDS1, BA	182.27	15.54
		PD, e^H, NMDS1, NMDS2, BA	182.28	15.55
		FR, PD, e^H, NMDS2, BA	182.93	16.20
		FR, PD, e^H, NMDS1, NMDS2	187.66	20.93
		Full model	188.12	21.39
	Zeroes	FR, PD, e^H, NMDS2, BA	131.27	0.00
		FR, e^H, NMDS1, NMDS2, BA	133.18	1.91
		Full model	133.46	2.19
		FR, PD, e^H, NMDS1, NMDS2	138.05	6.78
		PD, e^H, NMDS1, NMDS2, BA	137.50	6.23
		FR, PD, NMDS1, NMDS2, BA	137.96	6.69
		FR, PD, e^H , NMDS1, BA	143.48	12.21

*reported values correspond to the comparison with the best model.
Vegetation attributes: FR- floristic richness; PD- plant density; e^H – exponential form of Shannon's entropy index; NMDS1/2- first/second NMDS axis summarizing floristic composition; BA- total basal area.

Nest Abundance and Vegetation Attributes

Considering the entire floristic assemblage, a zero-altered negative binomial (ZANB) GLMM was the best-fitted model based on AICc (Table SIII). The ZANB GLMM that contained all explanatory variables (i.e. floristic richness, diversity and composition, and total basal area) except plant density was the one best supported for nest counts (Table II). Chimpanzee nest abundance was negatively correlated with floristic diversity (e^H) and total basal area, whereas positive associations were found with floristic richness and both NMDS axes summarizing floristic composition (Table III). Regarding the binary component of the model, significant parameter estimates were only obtained for e^H and plant density, suggesting that the probability of finding a zero decreases with increasing floristic diversity, but slightly increases with plant density (Table III).

TABLE III. Summary of GLMM Zero-Altered Negative Binomial Regression (ZANB) Models for Effects of Vegetation Attributes on Chimpanzee Nest Abundance, Considering the Entire Floristic Assemblage and Plant Species Known to be Eaten by LCNP Chimpanzees (see Table SI). Parameter Estimates (β) and Respective Standard Error (SE), z-Statistic and P-Value, are Shown Only for the Best-Ranked Models as Given in Table II.

Sample	Parameter type	Variable	β	SE	*z*	P-*value*
Entire floristic assemblage	Nest counts	FR	0.333	0.083	4.02	<0.001
		e^H	-0.970	0.243	-3.99	<0.001
		NMDS1	0.964	0.189	5.09	<0.001
		NMDS2	4.917	1.218	4.04	<0.001
		BA	-0.006	0.001	-5.18	<0.001
		Intercept	5.805	0.876	6.62	<0.001
	Zeroes	PD	0.085	0.034	2.49	<0.05
		e^H	-0.350	0.121	-2.88	<0.01
		NMDS1	0.602	0.369	1.63	0.103
		Intercept	-1.063	1.968	-0.54	0.59
Food plant species	Nest counts	BA	-0.463	0.196	-2.36	<0.05
		Intercept	2.303	0.379	6.08	<0.001
	Zeroes	FR	0.518	0.163	3.18	<0.01
		PD	-0.056	0.029	-1.90	0.057
		e^H	-0.657	0.228	-2.89	<0.01
		NMDS2	2.848	0.884	3.22	<0.01
		BA	1.058	0.410	2.58	<0.01
		Intercept	-3.813	1.128	-3.38	<0.001

Vegetation attributes: FR- floristic richness; PD- plant density; e^H – exponential form of Shannon's entropy index; NMDS1/2- first/second NMDS axis summarizing floristic composition; BA- total basal area.

Restricting the analysis only to food plant species, a ZANB GLMM again fitted our data best (Table SIII). For nest counts, the best model contained only total basal area of food tree species, showing a negative correlation between this predictor and nest abundance (Table II and III). This model further included floristic richness, e^H, NMDS2, and total basal area as important variables for explaining the occurrence of zeroes, suggesting that the probability of finding a zero increases with an increase in floristic richness, NMDS2, and total basal area, but decreases with e^H (Table III).

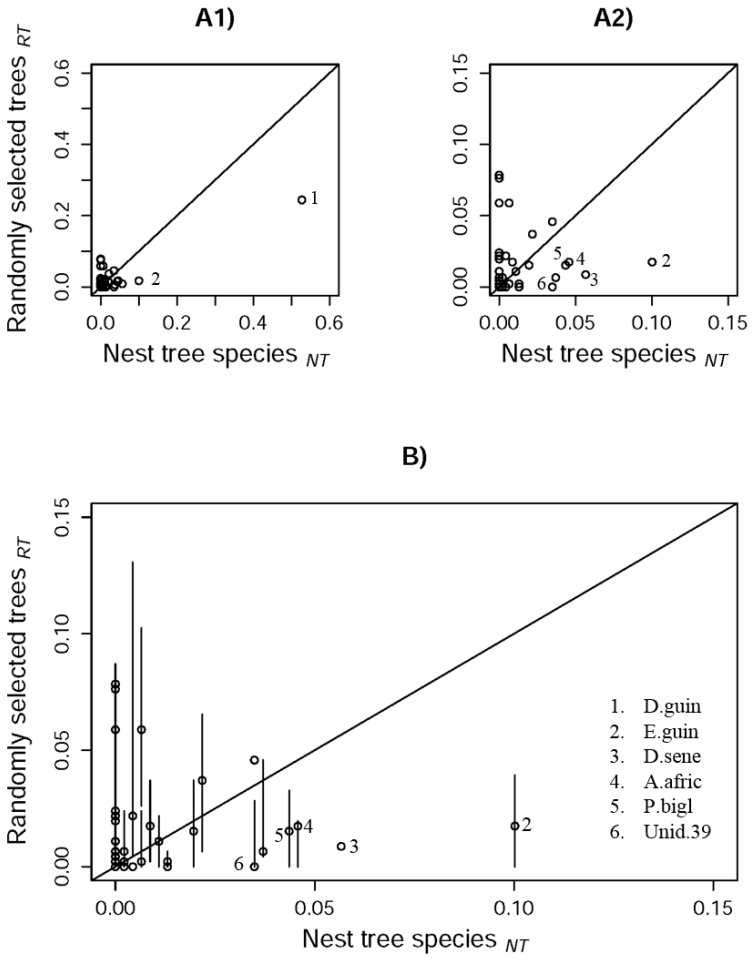

Figure 4. Expected proportions of trees with nests, if selection was random, as a function of observed proportions of nest tree species: (A1) considering all tree species or (A2) excluding *D. guineense*; and (B) distribution of expected proportions based on random sampling with replacement (1000x). Tree species: see Table SI.

Nest Tree Species Choice

Chimpanzees used 23 out of a total of 89 available tree species for nest building, which comprised, in addition to the tree species found during the vegetation surveys, five species that were only recorded during nest surveys (Fig. S4; compare Table I and Table SI). The tree species most chosen for nesting, *D. guineense* (52.7%), was also the most abundant (23.1%) in the study area (Fig. S4; Table I and Table SI). Comparing the proportions of tree species used for nesting and tree availability, *D. guineense*, *A. africana*, *D. senegalense*, *E. guineensis*, *P. biglobosa* and unidentified species 39 were clearly selected more often than expected by chance, hence being preferred tree species (i.e. located below the 1:1 line, see Fig. 4A1-2). In contrast, 17 species were used less frequently than expected based on their availability (i.e. found above the 1:1 line, see Fig. 4A1-2) and thus appear to be avoided for nesting. Based on the resampling procedure, for most trees used for nesting the proportions of randomly selected trees did not cross the 1:1 line, confirming a non-random choice of nest tree species by chimpanzees (Fig. 4B).

3.4 Discussion

This paper reports the first detailed quantitative data on nesting patterns of LCNP chimpanzees. During the dry season, chimpanzees built nests preferentially in dense forest (Carvalho et al. 2013), similar to what has been reported for other West African sites (Baldwin et al. 1981, Pruetz et al. 2008, Fleury-Brugiere and Brugiere 2010, Sousa et al. 2011). At their easternmost limit of distribution in Issa (Tanzania), despite no evident preference for forest or woodland, most nests were found in woodland even during the dry season (Hernandez-Aguilar 2009). Estimates of chimpanzee density at LCNP show an inverse relationship with habitat availability (Carvalho et al. 2013), highlighting that dense forest, although the least available habitat type in the park, offers the most suitable nesting conditions. Such conditions could include the availability of materials adequate for nest building (Koops et al. 2012a), the distribution and availability of food resources (Furuichi and Hashimoto 2004), and a lower incidence of human disturbance in dense forest compared to other habitat types (Last and Muh 2013). While we do not have data to evaluate the role of the first two factors, a negative influence of human disturbance on chimpanzee distribution at LCNP was demonstrated based on the distances between nests or habitat types and proxies of human disturbance (i.e. settlements, roads and rivers), suggesting that human disturbance is

lower in dense forest relative to the other habitat types (Carvalho et al. 2013). Nesting conditions in dense forest may also be more suitable due to the greater year-round availability of water, in contrast to savannah-woodland where most water sources dry up during the dry season (IBAP 2008).

Chimpanzee nest abundance was negatively related to floristic diversity and tree basal area, reflecting the preference for dense forest, the habitat characterized by comparatively lower diversity and a greater availability of smaller-sized trees. The positive correlation between nest abundance and floristic richness and composition, however, highlights that the other more open and species-rich habitats also play an important role in chimpanzee nest building. Studies on atelid (Cristóbal-Azkarate et al. 2005, Stevenson 2011) and cercopithecid monkeys (Rovero and Struhsaker 2007, Linder and Lawler 2012) found that primate abundance is positively associated with floristic diversity and total basal area, in contrast with our findings, and with floristic richness and composition, in line with our results. To the best of our knowledge, there are no comparable studies on chimpanzees that have related nest abundance with the comprehensive set of vegetation characteristics explored herein. Plant density was not a significant predictor of chimpanzee nest abundance in our study, in line with findings from Kalinzu Forest (Uganda) (Furuichi and Hashimoto 2004), where other predictors such as fruit abundance and vegetation type best explained chimpanzee nest abundance. Human activities have been contributing to the change in floristic richness, diversity, and composition in LCNP, as is typical for other African forests such as Kibale (Uganda) (Mitani et al. 2000), which have been recovering from decades or centuries of human disturbance. LCNP is a forest-savannah mosaic widely disturbed by humans and consequently current patterns of floristic richness, diversity, and composition are strongly shaped by everyday life activities and agro-ecological management by the park residents (IBAP 2008), as also reported from Kissidougou (Republic of Guinea) (Fairhead and Leach 1996). Over the last decades, the social, economic, and demographic changes in Guinea-Bissau have altered the extent to which sustainable land use has been practiced. Nowadays, dense forest is not well protected but often replaced by extensive monocultures of cashew (Barry et al. 2007, Carvalho et al. 2013). Thus, present-day distribution patterns of chimpanzees may reflect an adaptation to past human activities.

Typically, primate surveys have less than 100% detection probability, which leads to a possibly high frequency of zero counts. In our case, the probability of recording a zero was

associated with a number of predictor variables (floristic diversity and plant density) suggesting that some nests, specifically in dense forest, may not have been observed due to reduced visibility. Thus, the number of nests observed in dense forest and the preference for building nests in this type of habitat is likely even more pronounced than our nest count data indicate.

Our analysis restricted to food plant species showed that total basal area was negatively correlated with chimpanzee nest abundance, congruent with a preference for nesting in dense forest. In contrast, total basal area of food species was a positive predictor for *Cercocebus galeritus* abundance at Tana River Primate National Reserve (Kenya) (Wieczkowski 2004). Most nests (90%) at LCNP were built in feeding trees, similar to the proportion of nests (93%) at Bwindi National Park (Uganda) (Stanford and O'Malley 2008). Similar to our study, no data were collected on whether nest trees had ripe fruit at the time of observation or on physical characteristics of nest trees. According to Stanford and O´Malley (2008), chimpanzees may be selecting nest trees due to certain physical characteristics, such as tree height, maturity, among others, and not because they are feeding trees. Further research is clearly needed to determine whether tree physical characteristics in LCNP are having an effect on tree species selection for nesting.

We identified 23 tree species harboring chimpanzee nests at different proportions, of which *D. guineense*, *A. africana*, *D. senegalense*, *E. guineensis*, *P. biglobosa*, and one unidentified species (unidentified 39) were selected more often than expected by chance. In line with previous findings (Kalinzu Forest (Uganda), Furuichi and Hashimoto 2004), chimpanzees also nested in other ubiquitous tree species when preferred tree species were not available. Selectivity in the choice of nest tree species was also reported from other sites in Guinea, Uganda, and Tanzania (Furuichi and Hashimoto 2004, Ndimuligo 2007, Stanford and O'Malley 2008, Koops et al. 2012a). In Cantanhez National Park (CNP) in southern Guinea-Bissau, chimpanzees build nests preferentially (92%) in oil palms (*E. guineensis*) during the dry season (Gippoliti and Dell'Omo 1996, Sousa et al. 2011), in contrast to LCNP where it was the second most preferred species, albeit at a much lower proportion (10%). Other tree species such as *D. guineense* and *P. excelsa* (Sousa et al. 2011) are used for nesting by chimpanzees in both areas. Oil palm preference was also documented in Kounounkan Massif (Guinea) (Barnett et al. 1996), and in Bossou (Guinea) and Yealé (Ivory Coast) (Humle and Matsuzawa 2004). In contrast, no evidence for this was found at another Guinean site,

Seringbara (Humle and Matsuzawa 2004). Humle and Matsuzawa (2004) found that differences in oil-palm use between Bossou, Yealé and Seringbara could not be explained by environmental differences, but instead argued that patterns of oil-palm preference may be culturally determined. Since Yealé is a forested site, the findings of these authors are in contrast to Barnett et al.'s (1996) suggestion that oil palm preference could be an exclusive behaviour of marginal chimpanzee populations in West Africa that live in forest-savannah mosaics. Clearly, more data on oil palm use for nesting, particularly on oil palm density, from a greater range of study sites are necessary to be able to draw solid conclusions.

Based on our data, we cannot distinguish between two possible causes underlying the observed tree species preference. On the one hand, it could be a consequence of suitable habitat conditions offered by dense forest, for instance, in terms of resource availability, topographical features, or climatic conditions (Furuichi and Hashimoto 2004, Stanford and O'Malley 2008, Koops et al. 2012a). On the other hand, it could reflect the fact that chimpanzees preferentially select certain physical characteristics of trees (Baldwin et al. 1981, Pruetz et al. 2008, Hernandez-Aguilar et al. 2013) and those are predominantly found in tree species of dense forest.

Average nest height including *E. guineensis* or not was very similar (14.60 m and 14.01 m, respectively), and no significant differences were found among habitat types, although LCNP chimpanzees built nests higher in savannah-woodland than in forest habitats. Of the top two tree species preferentially used for nesting, *D. guineense* harbored nests at lower heights and at lower tree dbh than *E. guineensis*. If one considers the positive correlation found between nest height and tree dbh, nest tree species selection may be a consequence of different tree physiognomies. However, for several reasons this needs to be interpreted with caution. First, we used nest tree dbh as a proxy to infer nest tree height. However, the relationship between dbh and height is not always constant and comparison of tree dbh across study sites may not reflect a proportional difference in tree height (Hernandez-Aguilar et al. 2013). Secondly, nest height is better understood if compared to height distributions of trees with and without nests, as proposed by Pruetz et al. (2008) who found that chimpanzees select taller trees for nesting than expected based on the mean heights of available trees. Finally, variables such as nest tree height and the height of the lowest branch, among other characteristics, seem to better explain chimpanzee nest height, however, these data are currently only available for a

few study sites (Hernandez-Aguilar et al. 2013). We therefore advocate that such information be more routinely collected in future studies.

Irrespective of whether nests in *E. guineensis* were included or not, on average, we found that nest height at LCNP was considerably lower than what has been reported for CNP (14.6 m vs.19.7 m) (Sousa et al. 2011), but higher compared with reports from other countries across the subspecies' geographic range (see Hernandez-Aguilar et al. 2013). Lacking data on nest tree height or other tree physical characteristics for LCNP, we can only speculate whether the elevated nest height is actually a response to predator pressure in this park. Evidence that non-human predators still occur in Guinea-Bissau at abundances high enough to be considered a relevant threat to chimpanzees is limited, even though the presence of leopards is reported both for LCNP (IBAP 2008) and CNP (Gippoliti and Dell'Omo 1996). In CNP, nests in oil palm were located at the forest edge (i.e. in open-canopy habitats), reflecting, at least in part, that chimpanzees in this park are not directly persecuted by humans and generally do not avoid areas of human activity (Sousa et al. 2011, Hockings and Sousa 2012). The physiognomic characteristics and distribution of oil palms, which provide protection from predators (e.g. leopards), easier communication among group members, a wider view of the surrounding landscape, and proximity to specific resources for chimpanzees, were qualitatively attributed as the main causes for this preference in CNP (Gippoliti and Dell'Omo 1996, Sousa et al. 2011).

Arboreal nesting is generally interpreted as a strategy to avoid predation (Baldwin et al. 1981, McGrew 2004, Pruetz et al. 2008, Hernandez-Aguilar et al. 2013). However, in our case exclusive arboreal nesting could be related to human disturbance, similar to findings by Last and Muh (2013) who attributed the lack of ground nesting at one of their study sites to increased human pressure. Due to a local taboo, chimpanzees in Guinea-Bissau are supposedly not hunted owing to their similarities with humans (Gippoliti and Dell'Omo 2003). Nevertheless, LCNP residents reported that females are sometimes killed to sell their babies as pets, a scenario which has also been documented for the southern region of Tombali (Cá 2008). In Guinea-Bissau, body parts of chimpanzees have also recently been found to be used in traditional medicine (Sá et al. 2012). While this lends some support to the idea that exclusive arboreal nesting at LCNP may be a consequence of human disturbance, better quantitative data on non-human predators are needed to determine to what extent the construction of elevated nests is indeed a response to predators that can climb trees.

We are aware that our data only cover the dry season. Since an effect of seasonality on nesting patterns was documented for other West African sites (Assirik and Fongoli (Baldwin et al. 1981, Baldwin et al. 1982, Pruetz et al. 2008)) characterized by similar climatic conditions to those of LCNP, it would be important for future research to extend our work to include also the wet season to determine if patterns observed in this study hold over the full annual cycle.

Implications for Conservation

As shown, *D. guineense* is a key resource for LCNP chimpanzees, playing a central role in their nest building behavior. In 2011 we learned about a future local project that intends large-scale exploitation of this tree species for commercial timber harvesting (Nelson Dias, personal communication). As the remaining patches of dense forest in which this tree species occurs and suitable habitat conditions for chimpanzees are restricted to southern Guinea-Bissau, our results underline the importance of implementing effective conservation measures to mitigate the negative impacts of such exploitation on these forests, and consequently on one of the most threatened coastal chimpanzee populations.

Natural regeneration has been recommended following agricultural abandonment to recover forest structure and floristic composition (Aide et al. 2000). It is crucial that this traditional practice is maintained in this protected area as a low-cost strategy to restore dense forests. However, slash-and-burn agriculture needs to be regulated to enable colonization of seed sources from adjacent mature forests and to prevent soil degradation (Fairhead and Leach 1996, Aide et al. 2000). While these conservation efforts are foreseen in the forest law of Guinea-Bissau (Decree No. 4-A/91) an effective control by strengthening and enforcing the existing law will be important for these measures to succeed.

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Supporting Material

Table SI. Plant species densities (plant abundance /ha) per habitat and corresponding family. Also given is the mean diameter at breast height (dbh) for each species and whether it constitutes confirmed chimpanzee food at LCNP (Carvalho, unpublished data based on faecal analysis of samples collected during the dry season).

Plant species	Abreviation	Family	Density			Dbh (± SE)	Food species
TREES			DF	OF	SAV		
Afzelia africana	A.afric	Legum./Caesalp.	8.59	0.00	0.27	0.38(0.071)	Yes
Albizia dinklagei	A.dink	Legum./Mimos.	0.00	0.00	0.53	0.58(0.097)	Yes
Albizia zygia	A.zygi	Legum./Mimos.	8.59	0.00	1.33	0.18(0.017)	-
Alstonia boonei	A.boon	Apocynaceae	0.00	0.00	0.27	0.30	-
Anthostema senegalense	A.sene	Euphorbiaceae	40.80	20.45	1.60	0.17(0.006)	-
Antiaris toxicaria subsp. welwitschii	A.toxi	Moraceae	4.29	1.52	6.41	0.26(0.035)	Yes
Antidesma membranaceum	A.memb	Euphorbiaceae	9.31	0.00	0.53	0.14(0.010)	-
Borassus aethiopum	B.aeth	Palmae	0.00	1.52	2.40	0.45(0.068)	Yes
Cassia sieberiana	C.sieb	Legum./Caesalp.	5.01	9.85	4.54	0.17(0.013)	-
Ceiba pentandra	C.pent	Bombacaceae	2.15	3.79	1.87	0.55(0.229)	Yes
Cola cordifolia	C.cord	Sterculiaceae	0.00	0.00	0.27	0.11	Yes
Combretum collinum subsp. binderianum	C.coll	Combretaceae	0.00	0.00	4.81	0.12(0.007)	-
Combretum nigricans	C.nigr	Combretaceae	3.58	6.06	42.71	0.19(0.010)	-
Dalbergia boehmii	D.boeh	Legum./Papil.	1.43	0.00	0.53	0.12(0.011)	-
Daniellia oliveri	D.oliv	Legum./Caesalp.	5.01	9.09	24.56	0.37(0.027)	Yes
Detarium senegalense	D.sene	Legum./Caesalp.	5.01	2.27	2.14	0.19(0.019)	Yes
Dialium guineense	D.guin	Legum./Caesalp.	234.79	96.97	1.87	0.16(0.003)	Yes
Dichrostachys cinerea subsp. platycarpa	D.cine	Legum./Mimos.	2.86	5.30	1.87	0.16(0.017)	-
Diospyros heudelotii	D.heud	Ebenaceae	5.01	0.00	0.00	0.14(0.013)	-
Elaeis guineensis	E.guin	Palmae	5.01	12.12	2.94	0.41(0.029)	Yes
Erythrina senegalensis	E.sene	Legum./Papil.	0.00	0.00	0.27	0.10	Yes
Erythrophleum suaveolens	E.suav	Legum./Caesalp.	7.87	0.00	1.87	0.22(0.028)	-
Ficus glumosa	F.glum	Moraceae	0.00	0.76	0.00	0.10	-
Ficus lutea	F.lute	Moraceae	21.47	3.79	0.53	0.32(0.051)	Yes
Ficus natalensis subsp. leprieuri	F.nata	Moraceae	0.00	0.76	0.00	0.60	-
Ficus polita	F.poli	Moraceae	0.00	6.06	4.00	0.36(0.077)	-
Ficus sur	F.sur	Moraceae	0.00	0.00	0.53	0.49(0.078)	Yes
Funtumia africana	F.afri	Apocynaceae	0.00	15.91	0.27	0.16(0.017)	-
Hexalobus monopetalus	H.mono	Annonaceae	0.00	0.00	0.53	0.11(0.010)	-

Khaya senegalensis	K.sene	Meliaceae	5.73	14.39	2.14	0.34(0.072)	-
Lannea acida	L.acid	Amaranthaceae	0.00	0.76	0.27	0.20(0.097)	-
Lophira lanceolata	L.lanc	Ochnaceae	0.00	0.00	0.27	0.30	-
Mitragyna inermis	M.inne	Rubiaceae	0.00	0.00	0.53	0.17(0.057)	-
Morinda geminata	M.gemi	Rubiaceae	0.00	1.52	1.60	0.36(0.107)	-
Newbouldia laevis	N.laev	Bignoniaceae	5.73	5.30	0.27	0.20(0.032)	-
Parinari excelsa	P.exce	Chrysobalanaceae	6.44	12.12	0.53	0.21(0.051)	Yes
Parkia biglobosa	P.bigl	Legum./Mimos.	2.15	3.03	5.61	0.31(0.040)	Yes
Pericopsis laxiflora	P.laxi	Legum./Papil.	0.00	0.00	0.27	0.13	-
Piliostigma thonningii	P.thon	Legum./Caesalp.	0.00	3.79	14.95	0.16(0.009)	Yes
Prosopis africana	P.afri	Legum./Mimos.	0.00	2.27	10.14	0.28(0.020)	Yes
Pterocarpus erinaceus	P.erin	Legum./Papil.	5.01	4.55	16.02	0.33(0.024)	Yes
Ricinus communis	R.comm	Euphorbiaceae	2.15	1.52	0.00	0.10 (0.004)	-
Spathodea campanulata	S.camp	Bignoniaceae	9.31	0.00	6.14	0.15(0.009)	-
Spondias mombin	S.momb	Anacardiaceae	11.45	6.06	4.81	0.23(0.011)	Yes
Terminalia macroptera	T.macr	Combretaceae	0.72	10.61	26.70	0.19(0.011)	-
Uvaria chamae	U.cham	Annonaceae	0.72	0.00	0.53	0.14(0.027)	Yes
unidentified 1	Unid.1	-	0.00	0.00	0.53	0.11(0.008)	-
unidentified 2	Unid.2	-	2.15	0.00	2.94	0.14(0.012)	-
unidentified 3	Unid.3	-	0.00	0.00	0.53	0.18(0.013)	-
unidentified 4	Unid.4	-	0.00	0.00	0.27	0.29	-
unidentified 5	Unid.5	-	0.00	0.76	0.80	0.24(0.024)	-
unidentified 6	Unid.6	-	0.00	0.00	1.33	0.11(0.004)	-
unidentified 7	Unid.7	-	0.00	0.00	1.07	0.15(0.016)	-
unidentified 8	Unid.8	-	0.00	0.00	0.27	0.11	-
unidentified 9	Unid.9	-	1.43	0.76	1.87	0.19(0.021)	-
unidentified 10	Unid.10	-	0.00	1.52	0.27	0.13(0.035)	-
unidentified 11	Unid.11	-	0.00	3.79	0.53	0.33(0.122)	-
unidentified 12	Unid.12	-	0.72	0.00	0.80	0.21(0.068)	-
unidentified 13	Unid.13	-	0.00	0.00	0.53	0.22(0.038)	-
unidentified 14	Unid.14	-	0.00	5.30	0.00	0.34(0.178)	-
unidentified 15	Unid.15	-	0.00	3.03	0.00	0.16(0.023)	-
unidentified 16	Unid.16	-	0.00	0.76	0.00	0.11	-
unidentified 17	Unid.17	-	1.43	0.00	0.27	0.16(0.030)	-
unidentified 18	Unid.18	-	0.72	0.00	0.00	0.16	-
unidentified 19	Unid.19	-	0.72	0.00	0.00	0.12	-
unidentified 20	Unid.20	-	0.00	0.00	0.27	0.11	-
unidentified 21	Unid.21	-	0.00	0.00	1.60	0.18(0.023)	-
unidentified 22	Unid.22	-	0.00	0.00	0.53	0.13(0.027)	-
unidentified 23	Unid.23	-	0.00	0.76	3.20	0.17(0.015)	-
unidentified 24	Unid.24	-	0.00	0.00	0.53	0.32(0.442)	-
unidentified 25	Unid.25	-	0.72	0.00	1.07	0.20(0.056)	-
unidentified 26	Unid.26	-	0.72	0.00	0.00	0.12	-
unidentified 27	Unid.27	-	0.00	1.52	0.00	0.29(0.167)	-
unidentified 28	Unid.28	-	0.00	0.00	0.27	0.10	-
unidentified 29	Unid.29	-	0.00	0.00	0.53	0.11(0.011)	-

unidentified 30	Unid.30	-	17.18	0.00	0.27	0.29(0.095)	-
unidentified 31	Unid.31	-	2.15	0.00	0.00	0.14(0.018)	-
unidentified 32	Unid.32	-	0.72	0.00	0.00	0.17	-
unidentified 33	Unid.33	-	3.58	0.00	2.40	0.19(0.017)	-
unidentified 34	Unid.34	-	28.63	0.00	19.75	0.16(0.005)	-
unidentified 35	Unid.35	-	0.00	0.00	0.27	0.20	-
unidentified 36	Unid.36	-	0.00	0.00	0.53	0.22(0.076)	-
unidentified 37	Unid.37	-	0.00	0.00	0.80	0.13(0.020)	-
unidentified 38	Unid.38	-	0.00	0.00	0.27	0.24	-
unidentified 42	Unid.42	-	0.00	6.82	0.00	0.17(0.015)	-
Total			481.03 [a]	286.36 [a]	244.79 [a]	0.22(0.009) [b]	[c]
LIANAS							
Combretum micranthum	C.micr	Combretaceae	2.86	0.00	2.14	0.13(0.011)	-
Cremaspora triflora	C.trif	Rubiaceae	0.72	0.00	0.00	0.22	-
Crotalaria hyssopifolia	C.hyss	Legum./Papil.	0.00	0.00	1.07	0.17(0.028)	-
Landolphia owariensis	L.owar	Apocynaceae	2.15	0.00	0.27	0.13(0.016)	-
Landolphia sp	L.sp	Apocynaceae	0.00	0.76	0.27	0.15(0.016)	Yes
Oxythenanthera abyssinica	O.abys	Dioscoreaceae	0.00	0.00	1.07	0.11(0.006)	-
Sarcocephalus latifolius	S.lati	Rubiaceae	0.00	0.76	0.00	0.11	Yes
Strophanthus hispidus	S.hisp	Apocynaceae	5.73	0.00	0.80	0.13(0.008)	-
Total			11.45 [d]	1.52 [d]	5.61 [d]	0.13(0.010) [e]	[f]

[a] Overall tree density averaged 304.19 trees /ha and differed significantly among habitats (Kruskal-Wallis test: χ^2 =10.90, df =2, P<0.05).

[b] Tree dbh varied between 0.19 (± 0.006) m and 0.23 (± 0.01) m in dense forest and open forest, respectively.

[c] Density of food trees averaged 190.6 trees /ha (range 97.2-312.1), without significant variation among habitats (Kruskal-Wallis test, χ^2 =5.18, df =2, P=0.07); tree dbh of food trees averaged 0.24 (± 0.01) [0.20 (± 0.01) and 0.28 (± 0.01) m in dense forest and savannah-woodland, respectively].

[d] Liana density averaged 18.57 lianas /ha and did not differ significantly among habitats (Kruskal-Wallis test: χ^2 =3.03, df =2, P=0.22).

[e] Liana dbh in open forest and savannah-woodland was 0.12 (± 0.01) m and 0.14 (± 0.04) m, respectively.

[f] Liana density averaged 0.59 lianas /ha (range 0.00-1.52), and no differences among habitats were found (Kruskal-Wallis test, χ^2 =4.33, df =2, P=0.11); liana dbh averaged 0.14 (± 0.02) m [0.12 (± 0.01) and 0.17 m in open forest and savannah-woodland, respectively].

Habitats: DF- dense forest; OF- open forest; SAV- savannah-woodland.

Tree (sub) family: Legum. – Leguminosae; Caesalp. – Caesalpinioideae; Mimos. – Mimosoideae; Papil. – Papilionoideae.

Table SII. Vegetation attributes of the successive habitat fragments encountered along the transects. Values are given per sampling unit (SU) standardized to relative density at 0.1ha considering either the entire floristic assemblage or those species known to be consumed by chimpanzees (see Table SI). Total area of each SU (ha) is also given.

Transect	SU habitat	Area	Entire floristic assemblage						Food plant species					
			FR[a]	e^{H} [b]	NMDS1	NMDS2	Density	BA[c]	FR[d]	e^{H} [e]	NMDS1	NMDS2	Density	BA[f]
A	SAV	1.40	44	18.82	-0.36	0.42	19.21	228.59	16	8.79	-0.60	-0.09	7.07	0.75
B	SAV	0.20	3	2.22	0.56	-0.10	3.50	78.07	1	1.00	0.77	-0.10	0.50	0.11
	OF	0.50	18	9.64	0.53	0.60	23.00	269.61	7	2.86	0.55	0.76	9.80	2.58
	OF	0.50	21	14.61	-2.21	-0.08	16.20	151.74	8	6.02	-1.33	1.04	5.80	0.32
F	SAV	0.80	26	11.41	0.83	0.03	31.13	318.82	8	5.13	0.72	0.20	13.13	0.90
	SAV	0.10	4	1.84	0.87	-0.17	19.00	157.08	3	3.00	0.98	-0.15	3.00	0.08
	OF	0.30	20	5.91	-1.12	0.66	46.00	486.51	11	2.81	-1.21	-0.07	34.67	1.45
	DF	0.20	21	8.49	-0.64	0.38	69.50	669.15	8	4.34	-0.88	0.42	35.00	2.32
G	SAV	0.06	9	6.99	1.25	-0.21	40.00	666.92	5	4.71	1.00	-0.25	11.67	2.69
	SAV	0.90	21	10.87	1.57	0.11	22.00	249.75	11	5.57	-0.60	-0.09	12.00	0.95
	OF	0.05	5	4.13	0.22	0.25	26.00	519.36	4	3.22	0.77	-0.10	22.00	1.66
	OF	0.07	11	9.20	-0.12	1.04	31.43	280.28	4	3.15	0.55	0.76	12.86	0.40
	DF	0.30	12	5.64	-0.26	0.78	23.00	232.62	3	1.90	-1.33	1.04	9.67	0.26
K	SAV	0.40	10	7.68	0.81	-0.58	38.75	355.02	9	5.83	0.72	0.20	8.00	1.39
	SAV	0.06	25	8.77	0.52	-0.57	28.33	327.25	5	4.33	0.98	-0.15	15.00	1.48
	DF	0.70	16	4.64	-0.50	-1.01	53.14	497.03	10	1.63	-1.21	-0.07	39.86	1.69
	DF	0.10	9	11.3	-0.73	-0.89	39.00	294.76	4	2.67	-0.88	0.42	12.00	0.28
	DF	0.20	27	4.85	-1.23	-0.64	34.5	350.48	4	3.83	1.00	-0.25	8.00	1.08

[a] Observed floristic richness for savannah-woodland was far greater (77 species, 938 individuals) than for the two types of forest habitat (dense forest: 44 species, 688 individuals; open forest: 40 species, 369 individuals).
[b] No significant differences were found among habitat types (Kruskal-Wallis test, χ^2 =0.576, df=2, P=0.75).
[c] Total basal area among SUs was significantly different (Kruskal-Wallis test, χ^2 =13.83, df =2, P<0.001).
[d] Observed floristic richness for savannah-woodland was far greater (21 species, 366 individuals) than for the two types of forest habitat (open forest: 16 species, 217 individuals; dense forest: 13 species, 436 individuals)
[e] No significant differences were found among habitat types (Kruskal-Wallis test, χ^2 =3.54, df =2, P=0.17).
[f] Total basal area among SUs was not significantly different (Kruskal-Wallis test, χ^2 =4.86, df =2, P=0.09).
Habitats: DF- dense forest; OF-open forest; SAV-savannah-woodland.
Vegetation attributes: FR- floristic richness; e^H - floristic diversity, expressed as the exponent of Shannon's index; NMDS1/2- first/second NMDS axis summarizing floristic composition; Density- plant density (plant abundance /0.1 ha); BA- total basal area (m^2 /0.1ha).

Table SIII. Comparison of model fit for different zero-inflated and hurdle models based on the sample-size corrected Akaike's Information Criterion (AICc), considering either the entire floristic assemblage or plant species known to be important in chimpanzee diet (see Table SI).

Sample	Model	AICc
Entire floristic assemblage	ZANB GLMM	174.71
	ZAP GLMM	191.54
	ZINB GLMM	305.07
	ZIP GLMM	338.98
Food plant species	ZANB GLMM	188.12
	ZAP GLMM	203.29
	ZINB GLMM	304.94
	ZIP GLMM	326.74

ZANB: zero-altered negative binomial.
GLMM: generalized linear mixed effects model.
ZAP: zero-altered Poisson.
ZINB: zero-inflated negative binomial.
ZIP: zero-inflated Poisson.

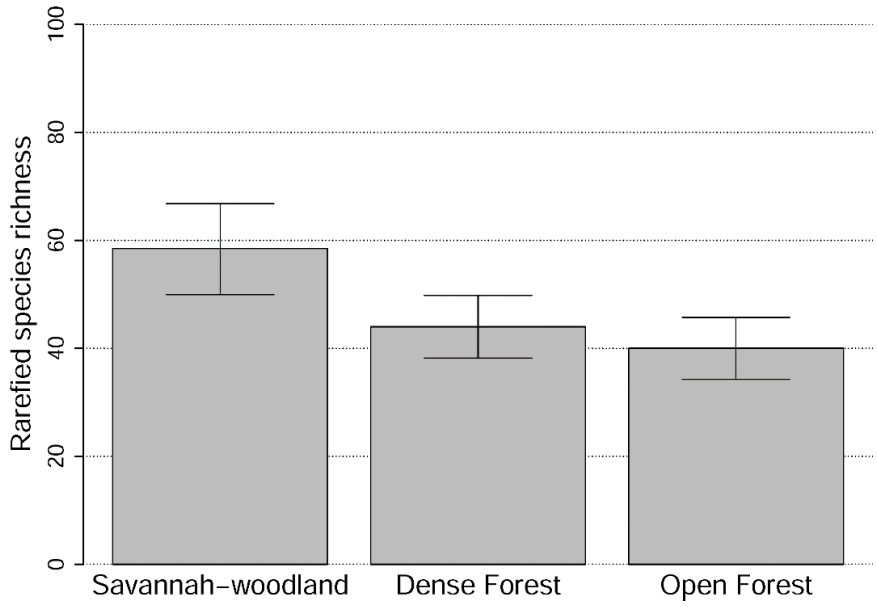

Figure S1. Comparison of rarefied species richness between habitat types based on the native floristic assemblage. Error bars represent 95% confidence intervals.

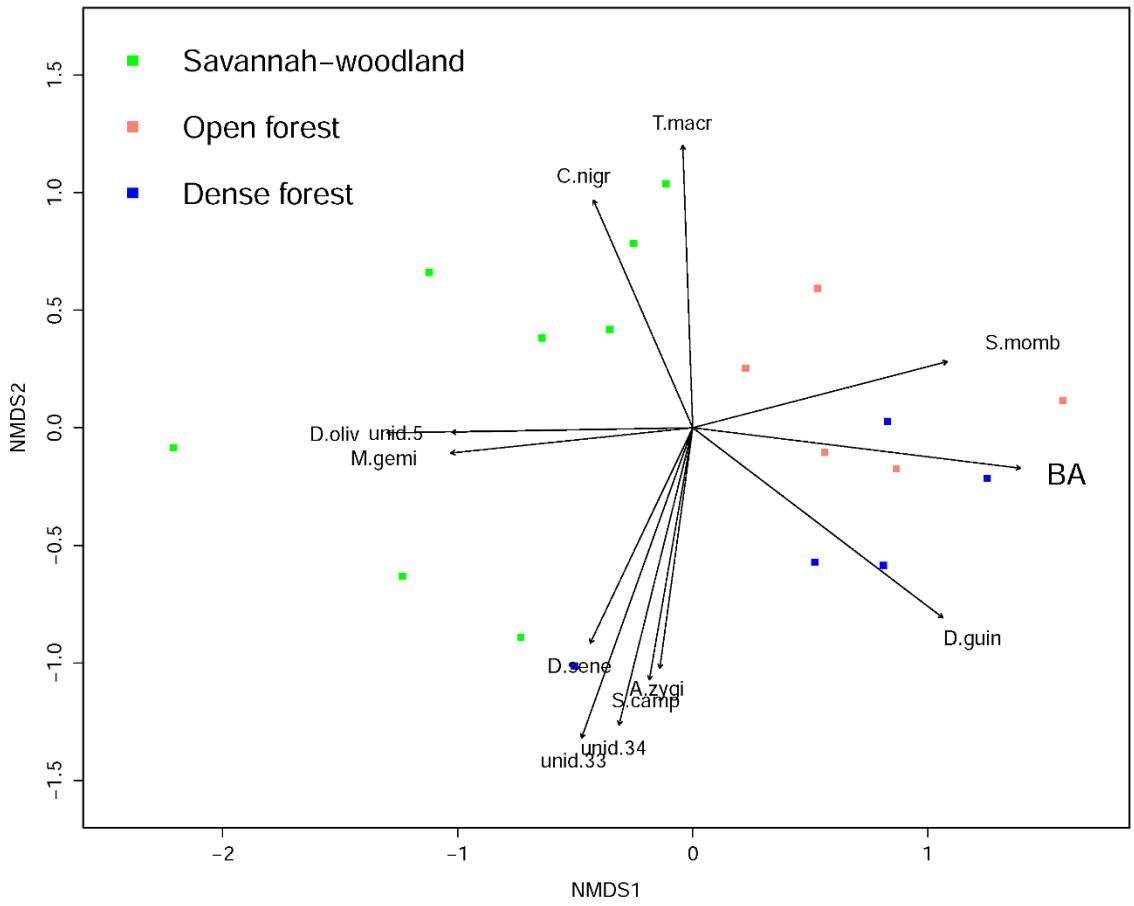

Figure S2. Ordination of sampling units along non-metric multidimensional scaling axes for the entire native floristic assemblage (stress=0.11). Vectors indicate species significantly correlated with the ordination axis (P<0.05). *Dialium guineense* showed a positive correlation with axis 1, *Terminalia macroptera* and *Combretum nigrans* were positively associated with axis 2, and *Spondias mombin* with both axes of the ordination. Total basal area (BA) was more closely associated with dense and open forests, however, the correlation with NMDS scores was not significant (R^2=0.16, P=0.27). Tree species: see Table SI.

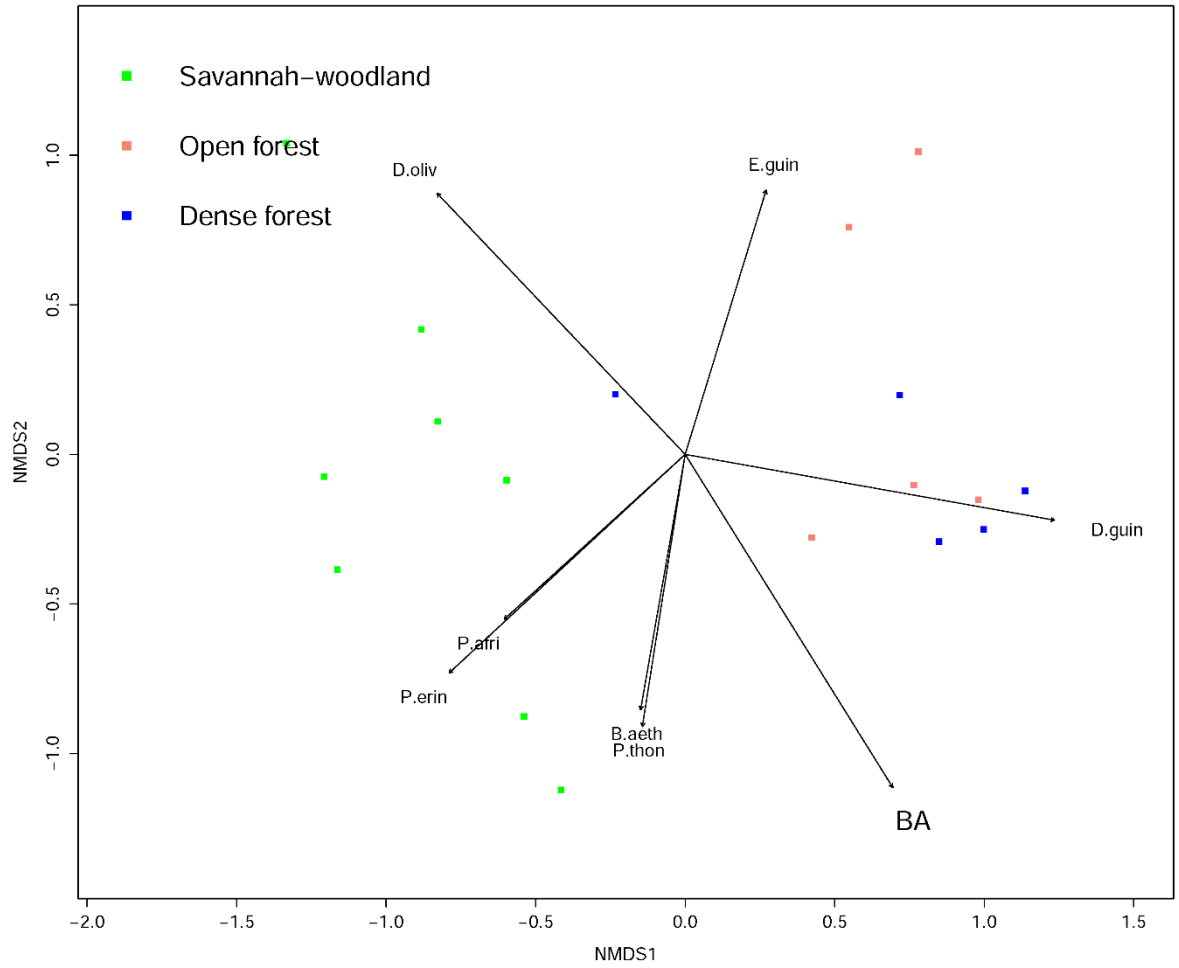

Figure S3. Ordination of sampling units along non-metric multidimensional scaling axes for species known to be locally important in the chimpanzees' diet (stress=0.18). Vectors indicate species significantly correlated with the ordination axis (P<0.05). The two-dimensional NMDS ordination showed similar patterns as for the entire native floristic assemblage (see Fig. 3). PERMANOVA confirmed that food plant assemblage composition differed significantly between habitat types (PERMANOVA, R^2=0.43, F= 5.59, P<0.001). Most of the feeding trees were negatively associated with NMDS axis 2, but *Dialium guineense* and *Daniellia oliveri* showed a positive relation with axis 1 and 2, respectively, and *Elaeis guineensis* with both axes. Total basal area (BA) did not differ among SUs (Kruskal-Wallis test, χ^2 =4.86, df =2, P=0.09) and no correlation was found with the ordination axes (R^2=0.09, P=0.47). Tree species: see Table SI.

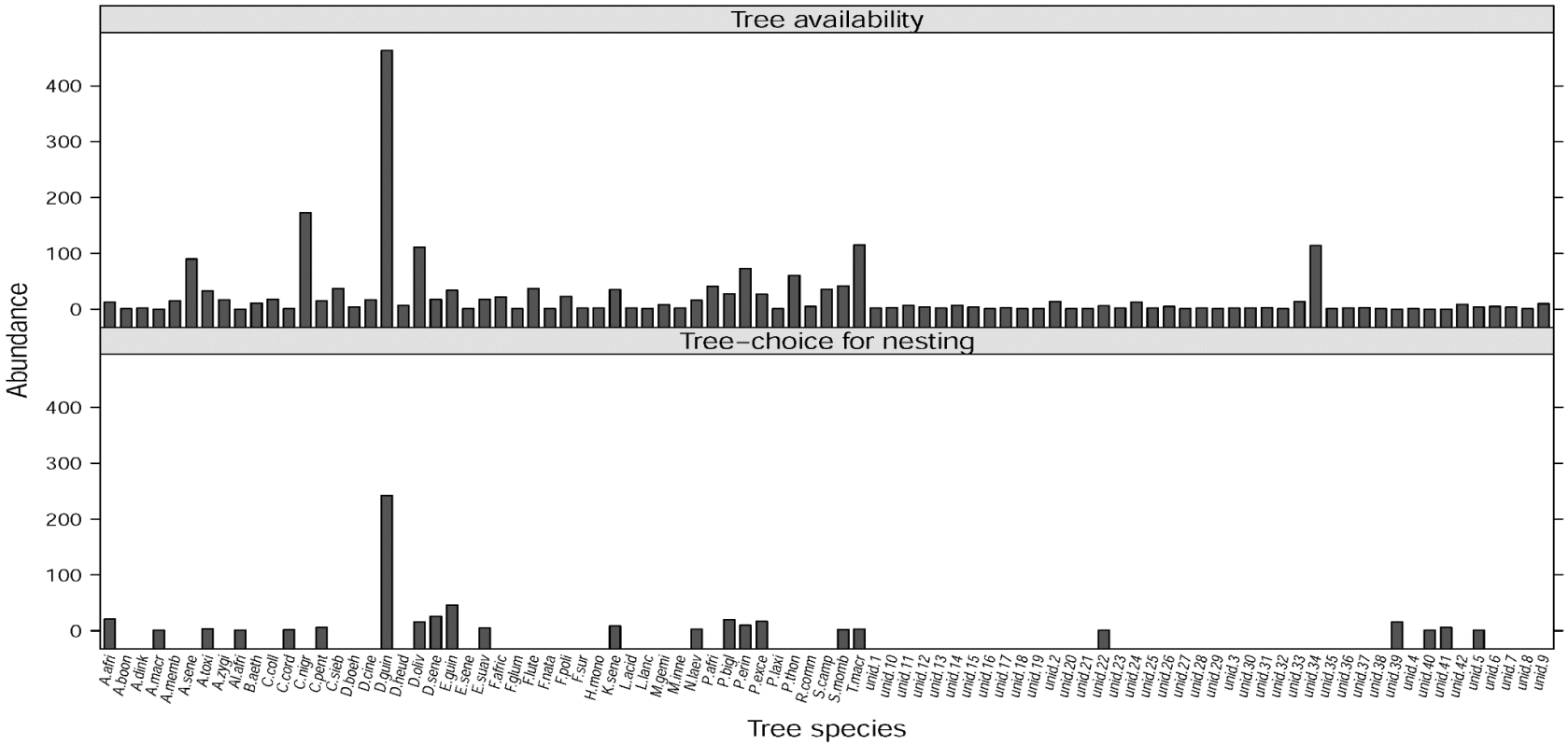

Figure S4. Tree species abundances recorded during vegetation surveys and tree species observed harboring chimpanzee nests.

Chapter 4

Chimpanzee Diet and Food Availability

Resumo

A disponibilidade alimentar determina a distribuição espacial e temporal das populações de chimpanzés. Entender os padrões fenológicos das espécies de plantas consumidas por esta espécie permite compreender os padrões de diversidade e composição da dieta dos chimpanzés. Caracterizados por uma dieta especializada, na qual os frutos maduros compreendem o principal alimento, os chimpanzés seleccionam algumas espécies de fruto desproporcionalmente à sua disponibilidade. Adicionalmente, folhas, flores, sementes, cascas, talos, mel, cogumelos, insectos, entre outros, podem fazer parte da sua dieta. Os chimpanzés podem também incluir na sua dieta frutos de espécies cultivadas e apresentar padrões de selectividade na escolha dessas espécies. Neste estudo, avaliou-se a variação espaço-temporal da disponibilidade alimentar e da riqueza, diversidade e composição dietária dos chimpanzés do Parque Natural das Lagoas de Cufada (PNLC, Guiné-Bissau). Um estudo fenológico foi conduzido de Março de 2011 a Fevereiro de 2012 através de uma amostragem focal de espécies de plantas. Amostras fecais e restos alimentares foram recolhidos apenas na estação seca de 2011. A maior disponibilidade de frutos ocorreu durante a estação seca e o pico de maturação da maioria das espécies de fruto foi registado antes do início da estação das chuvas. Os chimpanzés consumiram diferentes items de 31 espécies de plantas, representando 16 famílias. A dieta foi essencialmente composta por frutos e sua diversidade variou inversamente com a disponibilidade de frutos maduros ao longo da estação seca. Os chimpanzés foram bastante selectivos no consumo destas espécies, alimentando-se preferencialmente na floresta densa de frutos de *Spondias mombin* e *Uvaria chamae* no início da estação seca e de frutos de *Afzelia africana* a meio da estação seca. No final da estação seca, os chimpanzés consumiram preferencialmente frutos da floresta esparsa, nomeadamente de *Ficus* spp. e *Parinari excelsa*. Apesar das espécies de figueira serem normalmente consumidas pelos chimpanzés nos períodos de escassez alimentar, no PNLC estas espécies foram preferencialmente consumidas no período de maior abundância de frutos maduros. Espécies de plantas cultivadas foram também consumidas, ainda que a uma proporção menor relativamente ao consumo das espécies nativas. A composição dietária não variou com o aumento das distâncias geográficas entre fezes, realçando uma dieta generalizada entre os

chimpanzés do PNLC. Adicionalmente, nenhuma variação foi obtida entre a composição dietária e a proximidade a vilas ou estradas, *proxies* da presença de áreas de cultivo. Estes resultados sugerem que os chimpanzés do PNLC apresentam uma flexibilidade e plasticidade dietária, adaptando a sua dieta à variação sazonal da disponibilidade alimentar. Contudo, é de esperar que a substituição contínua dos seus habitats por áreas de cultivo aproxime cada vez mais os chimpanzés às comunidades locais, potenciando os conflitos entre estes e reduzindo a tolerância dos agricultores para com esta espécie. Deste modo, é importante delinear estratégias que minimizem quer o impacto dos chimpanzés nas áreas de cultivo quer o impacto das comunidades locais nas florestas densas, evitando assim a competição directa por recursos.

Palavras-chave: amostras fecais; dieta; disponibilidade alimentar; fenologia; figueira; frutos cultivados.

Paper III. Spatio-temporal variation in chimpanzee food availability and dietary composition in a human-dominated landscape

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Abstract - Knowledge about phenological patterns as principal determinants of food availability is important to understand spatial and temporal variation in chimpanzee abundance, habitat use, and diet. We assessed spatio-temporal variation in food availability and dietary richness, diversity and composition for chimpanzees at Lagoas de Cufada Natural Park (LCNP), Guinea-Bissau, a forest-savannah mosaic widely disturbed by humans. A phenological study was conducted from March 2011 to February 2012 by sampling focal plant taxa. Faecal samples and feeding remains were collected during the dry season of 2011. More fruits were available in the dry than in the wet season, and fruiting peaked at the onset of the rainy season. LCNP chimpanzees showed a fruit-based diet composed of 31 identified plant species representing 16 families. Dietary richness was inversely related to ripe fruit availability over the course of the dry season. Chimpanzees were very selective frugivores, feeding preferentially on fruits in dense-canopy forests, especially of *Spondias mombin* and *Uvaria chamae*, during the early dry season, and *Afzelia africana*, during the mid dry season, but switching to open forests in the late dry season where fruits of *Ficus* spp. and *Parinari excelsa* were abundant. There was no significant association between dietary composition and geographic distances among faecal samples, suggesting that chimpanzees have access to and largely use the same set of plant species over the entire study area. Moreover, no influence of settlements or roads as proxies for the presence of cultivated areas was found on dietary composition. Our findings highlight that chimpanzees show a plastic trophic behaviour, being able to adapt their diet to seasonal variation in food availability and human landscape modification. The latter is of particular interest because it suggests potential for increased human-primate interactions and conflict due to resource competition. Thus, for the long-term conservation of LCNP chimpanzees it will be important to balance their habitat requirements with the needs of local communities for agricultural land.

Key-words: crop food availability, diet, faecal samples, feeding ecology, phenology, western chimpanzee, wild food availability.

4.1 Introduction

Frugivores are widely abundant in the tropics, even though fruiting events and hence fruit availability are strongly seasonal (Fleming et al. 1987, Levey 1988, Chapman et al. 1999). In tropical forests, primates represent a large part of the frugivore biomass (Eisenberg and Thorington 1973, Tutin et al. 1991, Wrangham et al. 1994), and as both seed consumers and seed dispersers play an important role in ecosystem functioning (Lambert and Garber 1998). Recently, the ecological role of primates was extended to commensal associations with certain species of birds and mammals that follow primate groups to exploit dropped food and flushed prey (Heymann and Hsia 2014).

Increasing anthropogenic habitat loss, climate change, and human settlement of wild areas (Sekercioglu 2010) may negatively impact or disrupt ecosystem service provision (Ehrlich and Ehrlich 1981). Habitat loss and fragmentation have been approximating chimpanzees to humans, leading to the transmission of diseases and pathogens (Campbell et al. 2008). Throughout their range, suitable habitat for chimpanzees is increasingly surrounded by agricultural and agro-forestry areas, especially where there is a higher human population density (Campbell et al. 2008), often resulting in chimpanzee-human conflicts such as crop-raiding (Hockings et al. 2009). Few studies have provided insights into the diet and feeding ecology of chimpanzees in human-dominated landscapes (Hockings et al. 2009, Hockings and McLennan 2012, McLennan 2013). These studies suggest new feeding opportunities arising from crops, particularly the consumption of cultivated foods in periods of wild fruit scarcity. However, little is known about whether there are consistent shifts in dietary composition with respect to settlements or roads as proxies for the presence of agricultural areas.

Since food availability may determine spatial and temporal variation in chimpanzee distribution and abundance, and influence patterns of habitat use, knowledge about phenological patterns of plant species on which chimpanzees base their diet is crucial (Suzuki 1969, Baldwin et al. 1982, Tutin and Fernandez 1993). Phenological events are the plant biological activities over the course of an annual cycle, representing adaptations to the seasonality of biotic or abiotic factors (Aide 1992, van Schaik et al. 1993), which are often site-dependent (Chapman et al. 1999). Biotic processes such as high abundance of herbivorous insects may favor phenological convergence by determining the sharpness of the

peak of each phenophase; on the other hand, abiotic factors such as climate may regulate its timing (van Schaik et al. 1993).

The analysis of faecal samples is a commonly used tool for describing dietary patterns of many taxa: birds (Loiselle and Blake 1999), ungulates (Bodmer 1991), carnivores (Herrera 1989), bats (García-Morales et al. 2012), and primates (Chapman et al. 1995, Morgan and Sanz 2006), including chimpanzees (Tutin and Fernandez 1993, Basabose 2002, Moscovice et al. 2007). As ripe-fruit specialists, chimpanzees show an overwhelmingly plant-based diet, selecting fruits disproportionately to their overall availability (Tutin et al. 1997, Lambert and Garber 1998, Moscovice et al. 2007). In periods of habitat-wide fruit scarcity chimpanzees supplement their diet with foliage, flower, bark, piths, or even honey, mushrooms, insects or arthropods (McGrew et al. 1988, Wrangham et al. 1998, Basabose 2002, Watts et al. 2012a), which are considered fallback foods (FBF) (Wrangham et al. 1998, Marshall et al. 2009). Despite some controversy about what is the best definition of FBF (Lambert 2007, Marshall and Wrangham 2007), there is consensus that the same class of food may have different function in different primate species (Tutin et al. 1997, Marshall et al. 2009). Figs are a good example of FBFs in the diet of chimpanzees, as they reportedly also are for other apes such as gibbons (Marshall and Leighton 2006), orang-utans (Wich et al. 2004), and gorillas (Rogers et al. 1990). Another adaptation to seasonal variation in food availability is that chimpanzees often expand their home ranges in response to food scarcity (Baldwin et al. 1982, Chapman et al. 1995, Furuichi et al. 2001), as reported for other taxa such as birds (Karr 1976), insects (Janzen 1970) or certain fruit bats (Rollinson et al. 2013).

In this study, we characterized the spatio-temporal variation in plant food availability and diet for *Pan troglodytes verus* in a protected, but highly human-modified landscape in Guinea-Bissau. We hypothesized that dietary composition shows spatial variation among habitat types and temporal variation over the dry season. In particular, we predicted that 1) similarity in diet composition would be greater within habitat types (dense forest, open forest, savannah-woodland) and within dry season periods (early, mid, late) than between habitats and periods, 2) similarity in diet composition decreases with increasing geographic distance among faecal samples, and 3) the proximity to agricultural areas influences diet composition due to the increasing consumption of crop species. Moreover, we expected dietary richness and diversity to vary temporally according to fruit availability over the dry season. Specifically, we predicted that 4) chimpanzee diet would be fruit-dominated, but less diverse

during periods of high fruit availability, i.e. in periods when fruit abundance is highest chimpanzees should focus on a smaller subset of fruit species, and 5) fruit consumption is non-random with respect to availability and chimpanzees preferentially select certain fruit species from those available.

4.2 Methods

Study Site and Study Species

Lagoas de Cufada Natural Park (LCNP, between 11º34' and 11º51' N and 14º49' and 15º16'W) is a protected area in Guinea-Bissau (Fig. 1), a small West African country located between the rainforests of the Gulf of Guinea and the Sahelian and Sudanese semi-arid zone of dry savannahs and open-canopy forests (Catarino et al. 2002). Savannah will be used throughout the paper synonymously with dry habitat. LCNP is characterized by a mean annual temperature of 26ºC, and an average annual rainfall of 2200 mm that falls mostly during the wet season (June-October), whereas almost no precipitation (<100 mm) occurs during the dry season (November-May) (Catarino et al. 2002; http://sdwebx.worldbank.org/climateportal/index.cfm). To better distinguish patterns of plant species consumption and availability, we separated the dry season into early dry season (EDS, October-December), mid dry season (MDS, January-February) and late dry season (LDS, March-May), and the wet season into early and late wet season (EWS, June-July; LWS, August-September).

LCNP comprises a forest-savannah mosaic that is widely disturbed by human activities. Most of the roads and settlements are surrounded by agricultural areas, particularly cashew plantations (Carvalho et al. 2013). Dense-canopy forests are distinguished by higher canopy coverage (ca. 90%) and an undeveloped understory, whereas open-canopy forests or savannah-woodlands are characterized by lower canopy cover (ca. 60-70% and 20-40%, respectively). For a detailed description of habitat structure, diversity and composition see (Catarino et al. 2002, 2006, Carvalho et al. 2014).

The Western chimpanzee *P. troglodytes verus* has been classified as Endangered on the IUCN Red List since 1988 (IUCN 2014). Its range encompasses nine West African countries, although it is already considered rare or close to extinction in four of them, including Guinea-Bissau (Kormos et al. 2003). This subspecies showed a considerable population reduction

over the last 20-30 years due to several reasons, all having human activities and/or infectious disease as their core basis. For LCNP, chimpanzee density was recently estimated to be 0.22 nest builders/km^2 (95% CI 0.08–0.62), corresponding to 137 chimpanzees (95% CI 51.0–390.0) (Carvalho et al. 2013). The highest density was reported for dense-canopy forest, which despite being the least available and most threatened habitat type offers the most suitable habitat conditions and protection from human disturbance (Carvalho et al. 2013, 2014).

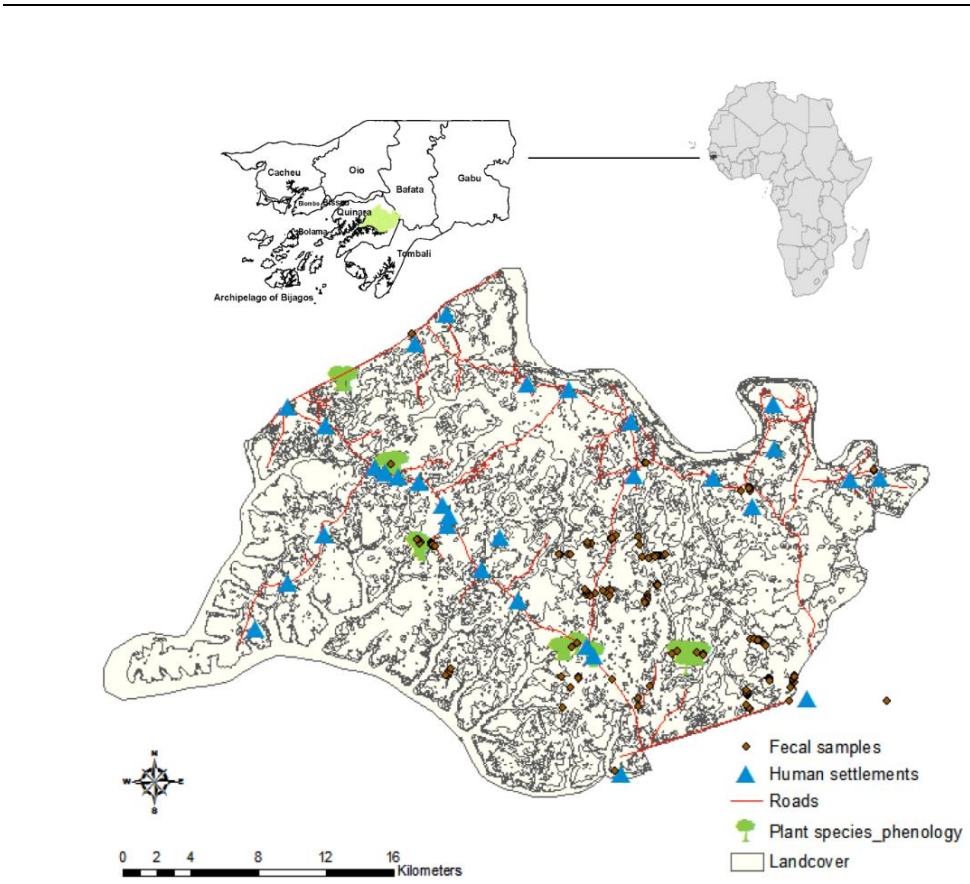

Figure 1. Sampling locations of the chimpanzee faeces collected in the protected area Lagoas de Cufada Natural Park, Guinea-Bissau. Also shown are the locations of human settlements, roads, and areas in the park where plant species were monitored along fruit trails.

Assessment of food availability

Before starting the phenological study we compiled a list of plant species known to be eaten by chimpanzees based on information provided by park guards and residents (see Table 1).

Based on this information, phenological data on focal plant taxa were recorded monthly, from March 2011 to February 2012 (Chapman et al. 1994, Marshall and Wich 2013). Trees of wild and cultivated species (with a diameter at breast height, dbh, >10 cm) and lianas (dbh >1cm) were randomly selected along trails that covered dense and open canopy forests, savannah-woodland, and cultivated areas (including settlements and cashew plantations). Phenological information on 346 individuals (298 trees, 30 herbs, 16 lianas and 2 shrubs) of 25 species from 14 families was monthly recorded (Table 1).

We noted the presence or absence of leaves, flowers, and fruits, and the corresponding phenological events (leaves and flowers: new/immature or old/mature; fruits: unripe or ripe). Additionally, we used visual counts to estimate the total number of fruits on a tree by counting the number of fruits in a subsection of the canopy selected *ad libitum* and then multiplying by the remaining subsections estimated to represent the total canopy area.

Chimpanzee diet

As chimpanzees in LCNP are very elusive, we relied on conventional analysis of faecal samples and feeding remains to describe their diet (Putman 1984, Basabose 2002, 2004). Although the analysis of faecal samples alone can neither fully reveal dietary composition nor allow a precise quantification of food items consumed, it is widely used as a nonintrusive method to examining the diet of vertebrates (Putman 1984, Donázar et al. 2010), including that of poorly habituated ape populations (Basabose 2004, Morgan and Sanz 2006). Over the dry season of 2011, 210 faecal samples were found, averaging 30±0.5 SE samples per month (range 7-68), by randomly wandering through both forest types, savannah-woodland, and agricultural areas. Each sample was collected in a plastic bag and the corresponding geographic location (using a Global Positioning System - GPS Garmin 60) and habitat type recorded. Then, faeces were sluiced in 1-mm mesh sieves, stored in a plastic bag and dried in sunlight. For each sample, the contents were divided into the following food items: fruits (including seeds, pulp, and fruit skins), foliage (fibers and digested fragments of leaves), flowers, fragments of insects, and other matter. Each food item was photographed, identified and preserved in paper bags containing silica gel. Identification of food items was carried out to the lowest level of taxonomic resolution possible. Except for figs, we counted all seeds present per sample. Some seeds, such as those of *Aframomum*, *Ficus*, and *Vitex*, were only identified to the genus level.

It is known that the chimpanzees also process fruits through wadging (Lambert 1999). From out of 10 direct chimpanzee observations in 2011, only in three cases feeding remains were found, i.e. wadges (N=29) and partially consumed fruits or foliage (N=9). Most feeding remains were identified on site and photographed. Feeding remains were only qualitatively considered to increase the list of plant species eaten by chimpanzees, especially by providing information on fibrous species that are difficult to identify by faecal analysis (Chancellor et al. 2012). Plant species identification was done with help from the park guards and other locals. When necessary, samples were collected for later identification at the herbarium of the *Instituto de Investigação Científica e Tropical* (Lisboa, Portugal). As animal-derived faecal matter, such as fragments of insects (N=8), parasites (N=2), bones (N=2), and hairs from small mammals (N=27), was difficult to identify, only plant material was considered for further analysis.

Table 1. List of the plant species monitored and eaten by chimpanzees, with the corresponding fruit availability index (FA_{sm}) by season and mean occurrence (%) of the plant species found in faeces.

Scientific Name (Abbreviation)	Family	Life Form	FA_{sm}		Item eaten			Occurrence (%)
Wild Species			Dry	Wet	Foliage	Flower	Fruit	
Adansonia digitata [1,2,3,4] (A.digi)	Bombacaceae	tree	0.67	-	-	-	-	-
Aframomum sp.[1] (Afram.spp)	Zingiberaceae	herb	-	-	-	-	F	2.30
Afzelia africana [2,3] (A.afri)	Legum./Caesalp.	tree	7.84	11.85	F	F	F,R	2.96
Allophylus africanus (Al.afri)	Sapindaceae	tree	-	-	-	-	F	0.58
Antiaris toxicaria [1] (A.toxi)	Moraceae	tree	8.00	8.00	F	-	F,R	11.15
Antisdesma membranaceum (A.memb)	Euphorbiaceae	tree	-	-	-	-	F	2.09
Borassus aethiopum [1] (B.aeth)	Palmae	tree	5.42	0.49	-	-	-	-
Ceiba pentandra [2,3] (C.pent)	Bombacaceae	tree	5.11	-	-	-	-	-
Cola cordifolia [2,3,4] (C.cord)	Sterculiaceae	tree	0.18	0.54	-	-	-	-
Daniellia oliveri [2,4]	Legum./Caesalp.	tree	27.50	-	-	-	-	-

(D.oliv)								
Detarium senegalense (D.sene)	Legum./Caesalp.	tree	8.75	12.50	-	-	-	-
Dialium guineense [1] (D.guin)	Legum./Caesalp.	tree	254.65	54.02	F,R	-	F,R	11.37
Elaeis guineensis [1,2] (E.guin)	Palmae	tree	28.50	14.00	F,R	F,R	F,R	7.74
Euphorbia schimperiana (E.schi)	Euphorbiaceae	herb	-	-	-	-	F	1.66
Ficus spp. [1,2,3,4] (Ficus.spp)	Moraceae	tree	4.88	-	F	-	F,R	14.42
Landolphia heudelotii [2,3] (L.heud)	Apocynaceae	liana	1.50	1.50	-	-	F	0.50
Mezoneuron benthamianum (M.bent)	Legum./Caesalp.	liana	-	-	-	-	F	0.33
Mucuna sp. (Mucuna.spp)	Legum./Papil.	liana	-	-	F	-	-	0.83
Neocarya macrophylla [1] (N.macr)	Chrysobalanaceae	tree	0.63	0.25	-	-	F,R	0.61
Parinari excelsa [1] (P.exce)	Chrysobalanaceae	tree	10.13	1.13	-	-	F,R	6.24
Parkia biglobosa [1,2,3,4] (P.bigl)	Legum./Mimos.	tree	3.11	3.11	F	-	R	0.24
Paullinia pinnata (P.pinn)	Sapindaceae	liana	-	-	F	-	F	0.20
Piliostigma thonningi [2,4] (P.thon)	Legum./Caesalp.	tree	-	-		-	F	0.08
Prosopis africana (P.afri)	Legum./Mimos.	tree	26.91	5.13	F	-	F	2.18
Pterocarpus erinaceus [2,4] (P.erin)	Legum./Papil.	tree	25.71	1.71	-	-	-	-
Ricinus communis (R.comm)	Euphorbiaceae	tree	-	-	F	-	-	0.73
Saba senegalensis [1,2,3,4] (S.sene)	Apocynaceae	liana	0.66	0.69	-	-	-	-
Spondias mombin [1,2,3,4] (S.momb)	Anacardiaceae	tree	1.19	26.08	-	-	F	4.16
Uapaca togoensis (U.togo)	Euphorbiaceae	tree	-	-	-	-	F	0.28
Uvaria chamae [1] (U.cham)	Annonaceae	shrub	1.13	-	-	-	F,R	9.30
Vitex sp. [1,3,4] (Vitex.spp)	Labiatae	tree	-	-	-	-	F	1.61
Voacanga africana (V.afri)	Apocynaceae	tree	-	-	-	-	F	0.30
Xylopia aethiopica (X.aeth)	Annonaceae	tree	-	-	F	-	F	0.66
Cultivated Species								
Anacardium occidentale (A.occi)	Anacardiaceae	tree	30.32	3.32	-	-	R	-

Carica papaya [1] (C.papa)	Caricaceae	tree	0.25	0.11	-	-	-	-
Citrus sinensis [1] (C.sine)	Rutaceae	tree	1.21	0.71	-	-	-	-
Hibiscus sabdariffa [1] (H.sabd)	Malvaceae	herb	-	-	F,R	-	-	0.25
Mangifera indica [1] (M.indi)	Anacardiaceae	tree	8.48	3.08	-	-	-	-
Musa paradisiaca [1] (M.para)	Musaceae	herb	0.38	0.28	F	-	-	0.55
Pennisetum glaucum (P.glau)	Gramineae	herb	-	-	F,R	-	-	0.08
Saccharum officinarum [1] (S.offi)	Gramineae	herb	-	-	R	-	-	-
Sorghum bicolor (S.bico)	Gramineae	herb	-	-	R	-	-	-
Unidentified Species								
unidentified 6 (unid6)*	-	-	-	-	-	-	F	0.71
unidentified 39 (unid39)*	-	-	-	-	F	-	F	0.33
Foliage unidentified (Foliage.unid) [4]	-	-	-	-	F	-		11.62
Flower unidentified (Flower.unid)	-	-	-	-	-	F	-	1.26
Fruit unidentified (Fruit.unid)	-	-	-	-	-	-	F	2.79

Type of data: F- Faecal sample; R- Feeding remains.
Also reported in [1]Cantanhez National Park (Sousa et al. 2013), [2]Fongoli (Senegal) (Bertolani and Pruetz 2011), [3]Assirik (Senegal) (McGrew et al. 1988), [4] Bafing Biosphere Reserve (Mali) (Duvall 2008).
*These species were previously described by Carvalho et al (2014).
Tree (sub) family: Legum. – Leguminosae; Caesalp. – Caesalpinioideae; Mimos. – Mimosoideae; Papil. – Papilionoideae.

Data analysis

All analyses were conducted in R version 3.0.2 (R Development Core Team 2013). Reported values are mean ±1SE unless otherwise noted**.**

Temporal variation in food availability

The percentage of phenological event *k* for phenological phase *p* in month *m* (P_{kpm}) was expressed as

$$P_{kpm} = \frac{\sum_{i=1}^{N} x_{kpmi}}{N_m} \times 100 \quad , \qquad (1)$$

where x_{kipm} represents the phenological event k in phenological phase p in month m for individual i and N_m corresponds to the total number of individuals in month m (k=1,…, K; p=1,…, O; m=1,…, M; i=1,…, N).

For each species in each month a fruit availability index (FA_{sm}) was calculated as

$$FA_{sm} = A_s \times \frac{Z_{sm}}{n_m} \quad , \qquad (2)$$

where A_s represents the abundance of species s found in previous vegetation surveys (see Carvalho et al. 2014), Z_{sm} corresponds to the number of individuals of species s (s=1,…, S) in month m observed in fruiting in phenological surveys and n_m represents the total number of individuals of species s in phenological surveys. For all direct comparisons with the faecal data phenological data were restricted to the dry season.

Spatio-temporal variation in diet

The proportion of a food item for each species in each faeces per month (P_{qsfm}) was assessed as

$$P_{qsfm} = \frac{y_{qsfm}}{\sum_{q=1}^{Q} \sum_{s=1}^{S} y_{qsfm}} \quad , \qquad (3)$$

where y_{qsfm} corresponds to the volume of food item q of the species s for faeces f in month m (q=1,…, Q; f=1,…, F).

We also calculated the mean percentage of each food item q for each species s per month m (P_{qsm}) as

$$P_{qsm} = \frac{\sum_{f=1}^{F_m} P_{qsfm}}{F_m} \times 100 \quad , \qquad (4)$$

where F_m represents the total number of faeces in month m.

The proportion of food item *q* in month *m* (P_{qm}) was calculated as

$$P_{qm} = \sum_{s=1}^{S} P_{qsm} \quad , \qquad (5)$$

Similarly, the proportion of species *s* in month *m* (P_{sm}) was obtained as

$$P_{sm} = \sum_{q=1}^{Q} P_{qsm} \quad , \qquad (6)$$

Finally, the mean fruit species occurrence in month *m* (P_m) in faeces was defined as

$$P_m = \sum_{s=1}^{S} P_{sm} \quad , \qquad (7)$$

Because of different faecal sample sizes per month, we used sample-based rarefaction (Gotelli and Colwell 2010) to calculate the species richness expected in a subset of samples. Sample-based rarefaction was computed using EstimateS software (Colwell 2013) and comparisons were made at N=7 faecal samples, the maximum number in common across dry season months. We assessed dietary diversity by calculating the exponential form of the commonly used Shannon index, e^H (Jost 2006). The non-parametric Kruskal-Wallis test was used to test for differences in dietary diversity among dry season periods.

Dietary composition was explored by month, to assess temporal variability throughout the dry season, and by habitat type, which represents a gradient in canopy cover from savannah-woodland over open- to dense-canopy forest. Non-metric multidimensional scaling (NMDS) on a Bray-Curtis distance matrix was used to visualize variation in dietary composition (Legendre and Legendre 1998). NMDS is a robust non-linear ordination technique which preserves the distance relationships in a low-dimensional space, evaluating how good the *m*-dimensional configuration is through the stress (see Legendre and Legendre 1998, Zuur et al. 2007). Statistical significance of variation in dietary composition among dry season periods and habitat types was investigated using analysis of similarities (ANOSIM), a non-parametric permutation test analogous to ANOVA for dissimilarity matrices (Legendre and Legendre 1998).

Using ARCMAP 9.3, the Euclidean distance was calculated among faecal samples, and between each faeces and settlements and roads (including main and secondary roads). On average, nearest neighbor distances between faecal samples were small (0.15 ±0.05 km), but distances between faeces and roads (1.12 ±0.08 km) and faeces and settlements (2.94 ±0.11 km) were greater (Fig. S1). All spatial layers were projected into Universe Transverse Mercator (UTM) Zone 28N. Environmental digital data were made available through the CARBOVEG project (http://carboveg-gb.dpp.pt/) or from Amaro (2011).

To assess whether dietary composition was spatially structured, we tested whether the matrix of Bray-Curtis distances calculated based on the occurrence of plant species in faecal samples was correlated with the matrix of geographic distances among faecal samples. We controlled for an effect of sampling month (matrix of Gower's distances), using a partial Mantel test with 999 permutations (Mantel 1967, Manly 1997). Canonical correspondence analysis (CCA) (ter Braak 1986, ter Braak 1987, ter Braak and Verdonschot 1995), a multivariate direct gradient analysis technique, was used to examine the relationship between dietary composition and four explanatory variables: habitat type, month, distances to roads and to settlements. This eigenvector ordination technique was used to test for the amount of variation in chimpanzee diet explained by the canonical axes, i.e. linear combinations of these variables correlated to the occurrence of plant species (ter Braak and Verdonschot 1995, Legendre and Legendre 1998, Zuur et al. 2007). Overall statistical significance of the CCA was evaluated by a permutation test by comparing the observed CCA result with the distribution of CCA results from a large number of randomly shuffled data matrices (1000 times) (Legendre and Legendre 1998). An R function ("step.cca") provided by Dave Roberts at (http://ecology.msu.montana.edu/labdsv/R/labs/lab12/lab12.htm) was used to test for significance of individual environmental variables using a permutation approach. NMDS, ANOSIM, partial Mantel test, and CCA were performed using the package *vegan* (Oksanen et al. 2012).

Fruit consumption and availability

Linear regression was used to evaluate whether fruit consumption (i.e. mean fruit species occurrence per month in faeces or monthly dietary diversity) was positively correlated with dry season fruit availability (FA_{sm} index). Separate regressions were performed, one including

all fruit species and one including only species in common with those monitored during the phenological surveys.

A randomization test was implemented in R to investigate if the consumption of fruit species deviates significantly from a random selection of the fruit species available.

Samples of fruit species randomly selected from those available (random species: RS) were compared with fruit species eaten by chimpanzees (consumed species: CS). Random sampling with replacement was used to obtain RS samples (N=85.3, corresponding to the total of monthly occurrence of CS in faeces) from the fruit availability data (N=454.6, corresponding to the total of FA_{sm} index). This procedure was repeated 1000 times to evaluate how far from the expected proportion at random (p_{RS}) each observed proportion was (p_{CS}). For each fruit species, we obtained the distribution of consumption if that species were chosen at random (p_{RS}). Plotting the expected p_{RS} distribution as a function of observed p_{CS} allows one to distinguish preferred ($p_{CS}>p_{RS}$) fruit species from those consumed less frequently than expected based on their availability ($p_{CS}<p_{RS}$), depending on whether the distribution lies entirely below or above the 1:1 line, respectively. Overlap of the randomization distribution p_{RS} with the 1:1 line indicates that the observed p_{CS} might be observed as a result of random choice.

4.3 Results

Temporal variation in food availability

Leaf shedding and leaf flushing peaked during the early dry season (EDS) and mid dry season (MDS), respectively (Fig. S2). Overall, flower availability was greatest between MDS and the late dry season (LDS). Fruit availability was in line with the increase of fruit species richness during the dry season and the decrease over the wet season, and ripe fruit abundance peaked in LDS (Fig. S2 and S3). The FA_{sm} index generally followed the previously described pattern (Fig. 2). Individual species varied considerably in terms of the amount of ripe fruit provided and how fruit availability was temporally distributed over the annual cycle (Fig. S3). Only four species provided fruits year-round (Table 2, Fig. S3): *Landophia heudelotii*, *Saba senegalensis*, *Elaeis guineensis*, and *Musa paradisiaca*.

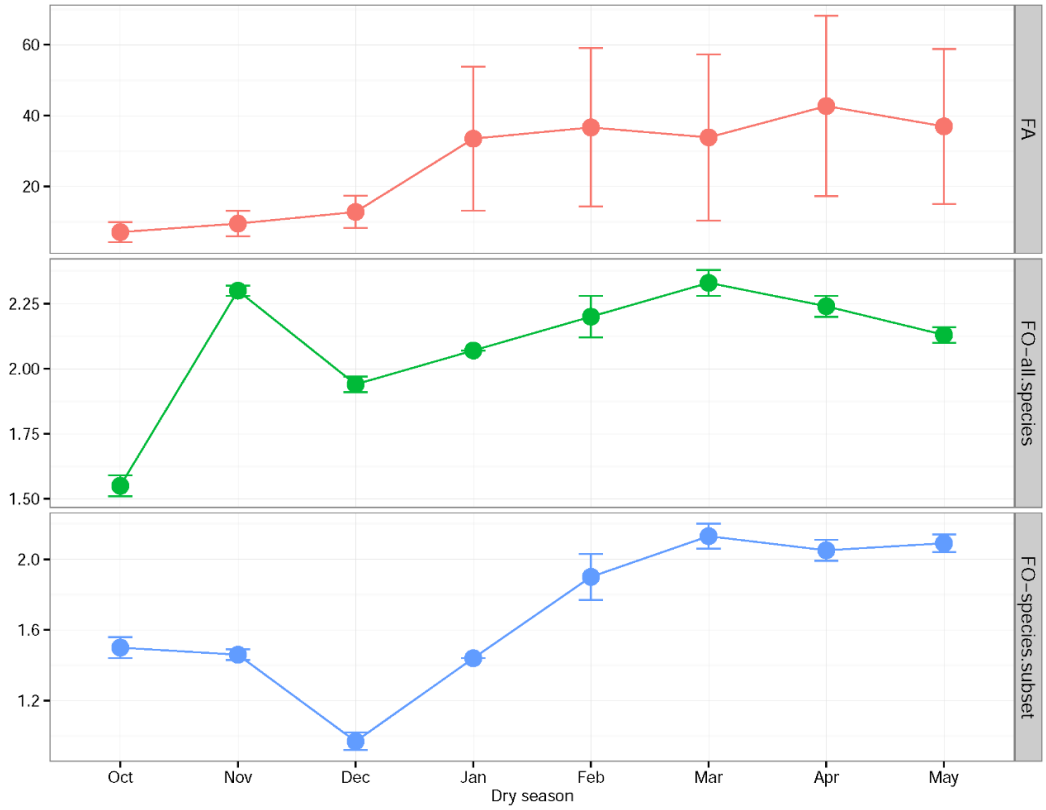

Figure 2. Mean (± SE) of fruit availability index (FA_{sm}) and fruit species occurrence in chimpanzee faeces during the dry season, either considering all fruit species (FO-all.species) or only species in common with those in phenological surveys (FO-species.subset). Only the *FA* index calculated using data for all fruit species is shown because the same trend for fruit availability over the dry season was found when only species in common with those in faeces were considered. Due to missing data for January, fruit occurrence in faeces for this month was imputed as the mean of fruit occurrence for December and February.

Spatio-temporal variation in diet

Overall, faecal samples were predominantly composed of fruit items (percent occurrence 72 ± 0.8%), followed by foliage (27 ± 0.6%) and flowers (1.0 ± 0.1%) (Fig. 3). Fruits dominated faecal samples during EDS and LDS, but were replaced by a higher proportion of foliage and flowers in MDS (Fig. 2 and 3). A total of 31 plant species were identified (N=28 from faecal samples; N=3 exclusively from feeding remains) representing 16 families (Table 1, Fig. S4). Most of these species belong to the legume subfamily Caesalpinioideae as well as to Euphorbiaceae and Gramineae. Wild species were the most recorded in faeces (82.4 ± 0.8%) and cultivated species were rarely found (0.9 ± 0.1%). Most of the food items belonged to

species of trees (67.2 ± 0.7%), followed by shrubs (9.3 %), herbs (4.8 ± 0.4%), and lianas (1.9 ± 0.1%). A total of 14 species were identified in feeding remains (N=38 samples), 11 of which were also found in faecal samples (Table 1).

Table 2. Fruit species selected by LCNP chimpanzees and used as fallback food (FBF), including their consumption in other study sites.

Scientific name	Forested sites[1]	Savannah/dry sites[2]
Selected plant species		
Afzelia africana	Mah	Ass
Afzelia spp.	-	Kas
Ficus spp.	Bel, Bul, Bwi, Gis, Gou, Kah, Kal, Kan, Lop, Mah, Ngo, Nyu, Oko, Rub	Ass, Baf, Bos, Fon, Iss, Kas
Parinari excelsa	Kah, Nyu, Ngo	Bos
Parinari spp.	Bwi, Mah, Rub	Iss, Kas
Spondias mombin	-	Ass, Baf, Bos
Uvaria chamae	-	-
Uvaria spp.	Bul, Kan, Mah, Rub	Kas
Fallback Foods (FBFs)		
Elaeis guineensis	Bos, Lop	-
Landolphia heudelotti	-	Ass, Fon
Landolphia spp.	Bel, Bul, Bwi, Gou, Kah, Kal, Mah, Nge, Oko	Bos, Iss, Kas
Musa paradisiaca	Oko	Bos
Musa spp.	Bel, Bul, Mah	-
Saba senegalensis	-	Ass, Baf, Fon
Saba spp.	Mah, Rub	Iss, Kas

[1] Bel= Belinga (Tutin and Fernandez 1985), Bul=Bulindi (McLennan 2013), Bwi=Bwindi (Stanford and Nkurununngi 2003), Gis=Gishwati (Chancellor et al. 2012), Gou= Goualougo (Morgan and Sanz 2006), Kah=Kahuzi (Basabose 2002, Yamagiwa and Basabose 2009), Kal=Kalinzu (Kagoro-Rugunda and Baranga 2008), Kan=Kanyawara (Wrangham et al. 1994, Wrangham et al. 1998, Lambert 1999, Chemurot et al. 2012), Lop=Lopé (Tutin et al. 1997), Mah=Mahale (Nishida and Shigeo 1983), Nge=Ngel Nyaki (Dutton et al. 2014), Ngo=Ngogo (Wrangham et al. 1994, Wrangham et al. 1998, Watts et al. 2012a), Nyu=Nyungwe (Gross-Camp et al. 2009) Oko=Okorobikó (Sabater-Pí 1979), Rub=Rubondo (Moscovice et al. 2007); [2] Ass=Assirik (McGrew et al. 1988); Baf=Bafing (Duvall 2008), Bos=Bossou (Sugiyama and Koman 1992, Humle and Matsuzawa 2004, Hockings et al. 2009), Fon=Fongoli (Bertolani and Pruetz 2011), Iss=Issa (Hernandez-Aguilar 2006, 2009), Kas=Kasakati (Suzuki 1969)

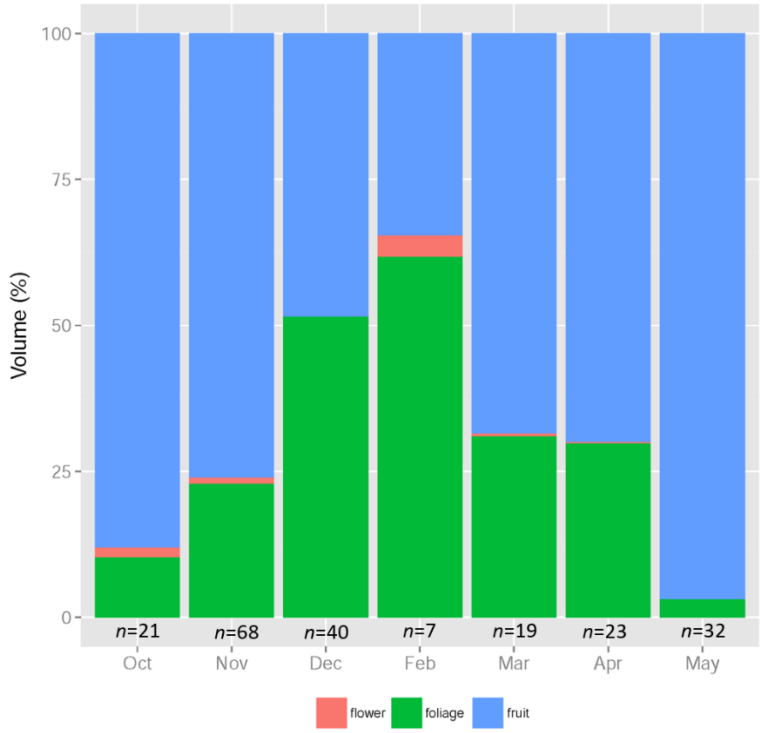

Figure 3. The percent volume of foliage, flowers, and fruits in chimpanzee faeces collected during the dry season. The number of faecal samples collected in each month is also provided. No data were recorded in January.

Dietary richness was greater in EDS ($N_{all\ spp}$=21, $N_{fruit\ spp}$=19) than in LDS ($N_{all\ spp}$= 13, $N_{fruit\ spp}$=10) or MDS ($N_{all\ spp=fruit\ spp}$=5) (Table 1, Fig. S4). However, sample-based rarefaction suggested no statistically significant difference in dietary richness between dry season periods (Fig. S5). Similarly, variation in dietary diversity was not significant among dry season periods (Kruskal-Wallis test, χ^2 =4.44, df =2, p=0.11).

There was considerable temporal variation in dietary composition. The two-dimensional NMDS ordination separated one group composed of faecal samples from MDS and LDS (February-May) and another one comprised of samples from EDS (October-December) along axis 1 (NMDS1; Fig. 4a). NMDS2 to a certain degree separated the samples from EDS and LDS from those of MDS. ANOSIM confirmed significant compositional variation in diet over the dry season (R=0.42, p<0.001). Ordinating samples spatially by habitat type, revealed

considerable variation in dietary composition along both NMDS axes and only loose clustering of samples by habitat (Fig. 4b). Variation in dietary composition among habitat types was significant based on ANOSIM, but had low explanatory power (R=0.12, p<0.001).

Dietary composition was not correlated with geographic distances among faecal samples (partial Mantel test: r= 0.002, p=0.44). The CCA indicated that the constraining explanatory variables (i.e. habitat type, month, distances to settlements and to roads) accounted for 7.23% of variation in dietary composition, and the first two canonical axes accounted for 88.1% of this variability. All explanatory variables were significantly associated with dietary composition (F=3.88, df=4, p<0.01). Axis 1 of the CCA (CCA1) was strongly and significantly associated with month (Δ eigenvalue=0.63, p<0.01) and with habitat type (Δ eigenvalue=0.12, p<0.05). CCA2 was associated with increasing distance to roads (Δ eigenvalue=0.05, p=0.71) and distance to settlements (Δ eigenvalue=0.05, p=0.71), but neither of these variables was significant (Fig. 5).

Fruit consumption and availability

Of the fruit tree species monitored in phenological surveys only about half (N=11, 44%) were also confirmed to be eaten by chimpanzees based on faecal analysis (Fig. 6). No significant association was found between the FA_{sm} index and mean monthly fruit species occurrence in faeces, irrespective of whether all (R^2=0.21, F=2.69, p=0.13) or only species in common with those in phenological surveys were considered (R^2=-0.11, F=0.29, p=0.61) (Fig. 2 and 6). Similarly, there was no significant effect of monthly fruit availability on dietary diversity (all fruit species: R^2=-0.11, F=0.30, p=0.60; fruit species in common: R^2=0.17, F=2.41, p=0.17).

Based on the resampling procedure, evidence for non-random selection of fruit species by chimpanzees was found for *Afzelia africana*, *Ficus* spp., *Parinari excelsa*, *Spondias mombin*, and *Uvaria chamae*, which were consumed at higher proportions than expected based on their availability (located below the 1:1 line; Table 2, Fig. 6 and 7). Plotting these selected species in the NMDS, revealed that *S. mombin* and *U. chamae* were associated with EDS and *A. Africana* with MDS along NMDS1. *Ficus* spp. and *P. excelsa* showed an association with LDS along NMDS2 (Fig. 4a). However, no clear pattern was found for habitat types (Fig. 4b).

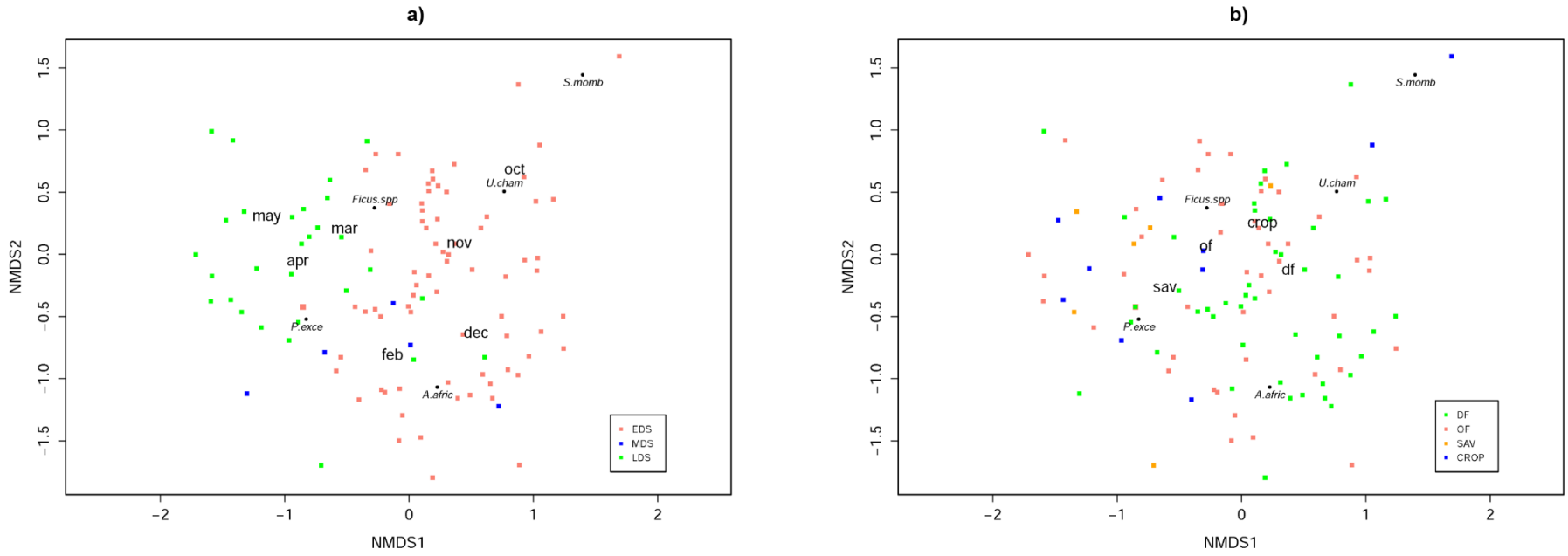

Figure 4. NMDS ordination of chimpanzee faecal samples a) by month and b) by habitat type where faeces were found (stress=0.09). Months and habitats are represented by centroids calculated based on occurrence data. For a better visualization only plant species with > 2 occurrences in the faecal samples were plotted (i.e. 24 species). Also shown are the fruit species selected by chimpanzees (see Figure 7). Plant species abbreviations: see Table 1. EDS: early dry season, MDS: mid dry season, LDS: late dry season, DF: dense canopy forest, OF: open canopy forest, SAV: savannah-woodland, CROP: cultivated areas.

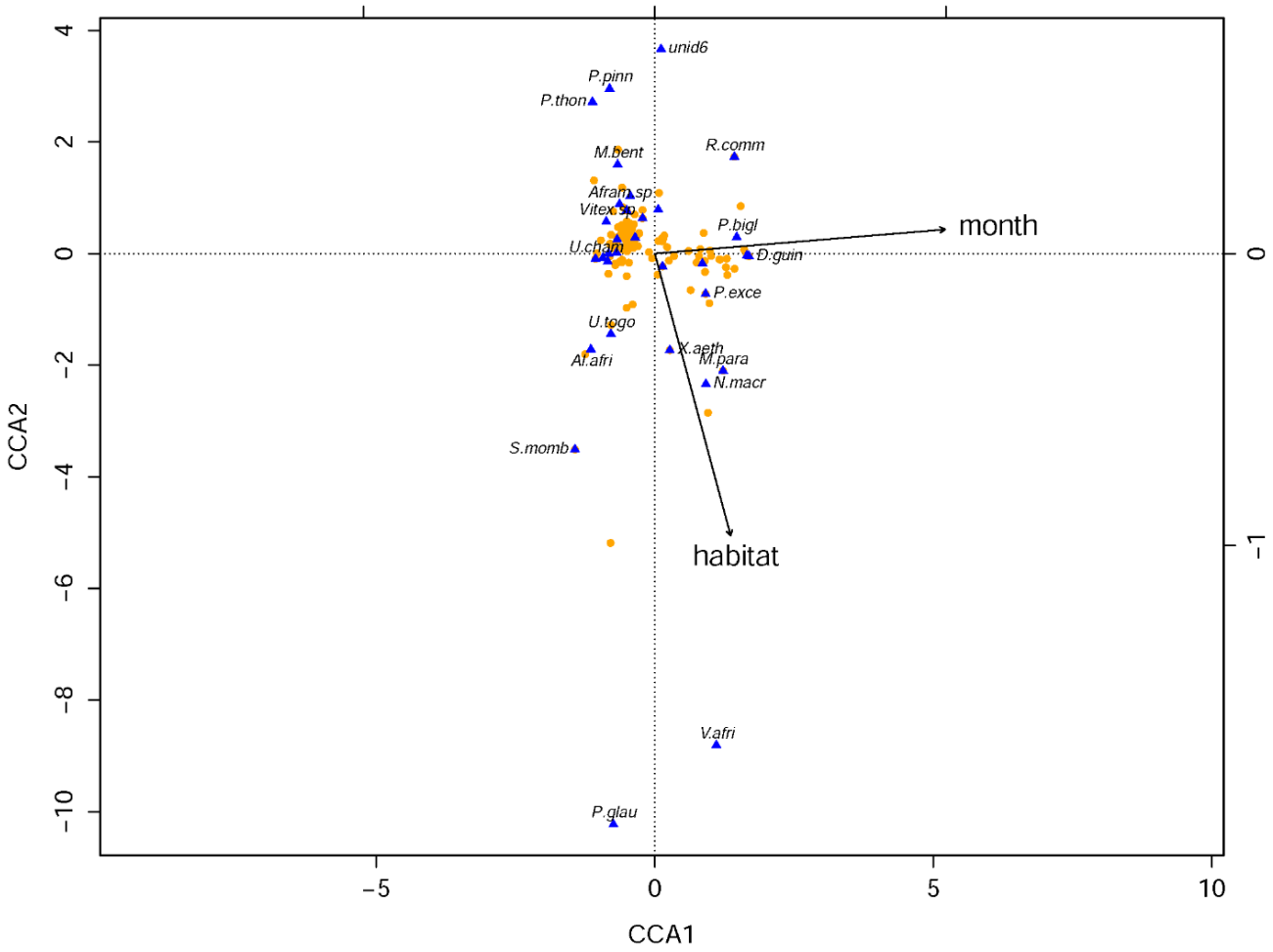

Figure 5. Canonical correspondence analysis triplot depicting variability in chimpanzee diet as explained by the environmental variables. Faecal samples (orange circles) were scaled as weighted averages of the species. Plant species are represented by blue triangles (not all species names were plotted for better visualization). Only significant explanatory variables ($p<0.05$) are shown by arrows (month: October-May; habitat: dense-canopy forest, open-canopy forest, savannah-woodland, and agricultural areas). Their length is proportional to the magnitude of the effect of that variable on the CCA axes, and the direction of the vector indicates the direction of the relationship between the variable and the CCA scores. The eigenvalues of axis 1 and axis 2 were 0.64 and 0.08, respectively. See Table 1 for species abbreviations.

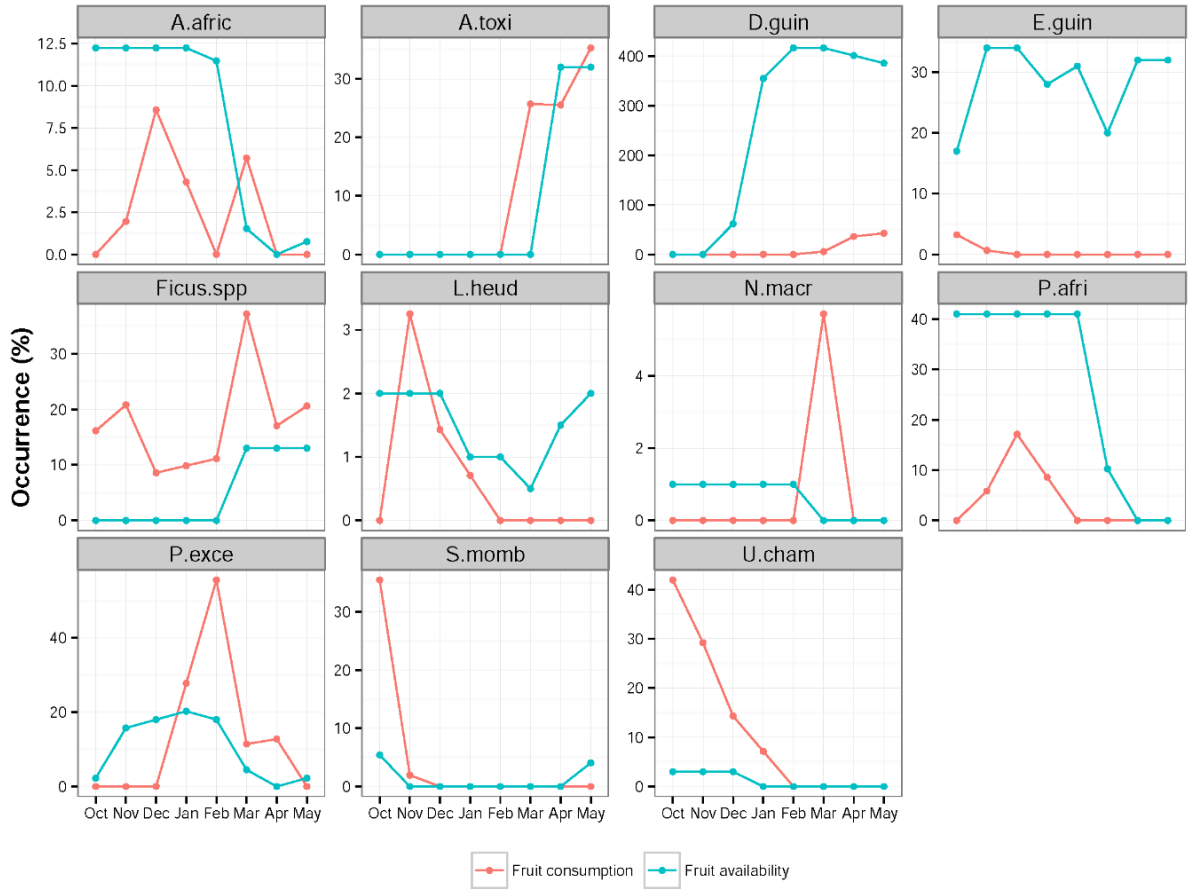

Figure 6. Comparison of the percentage of occurrence of fruit species availability (*FAsm* index) and fruit species consumption by chimpanzees during the dry season. For some species, such as *Afzelia africana*, *Antiaris toxicaria*, *Ficus spp.*, *Landolphia heudelotti*, *Neocarya macrophylla*, *Parinari excelsa*, *Spondias mombin*, and *Uvaria chamae*, fruit consumption exceeded its estimated availability during some periods of the dry season. Fruit occurrence in faeces for January represents the mean of fruit occurrence recorded for December and February. Note that the scale of the y-axis differs among species.

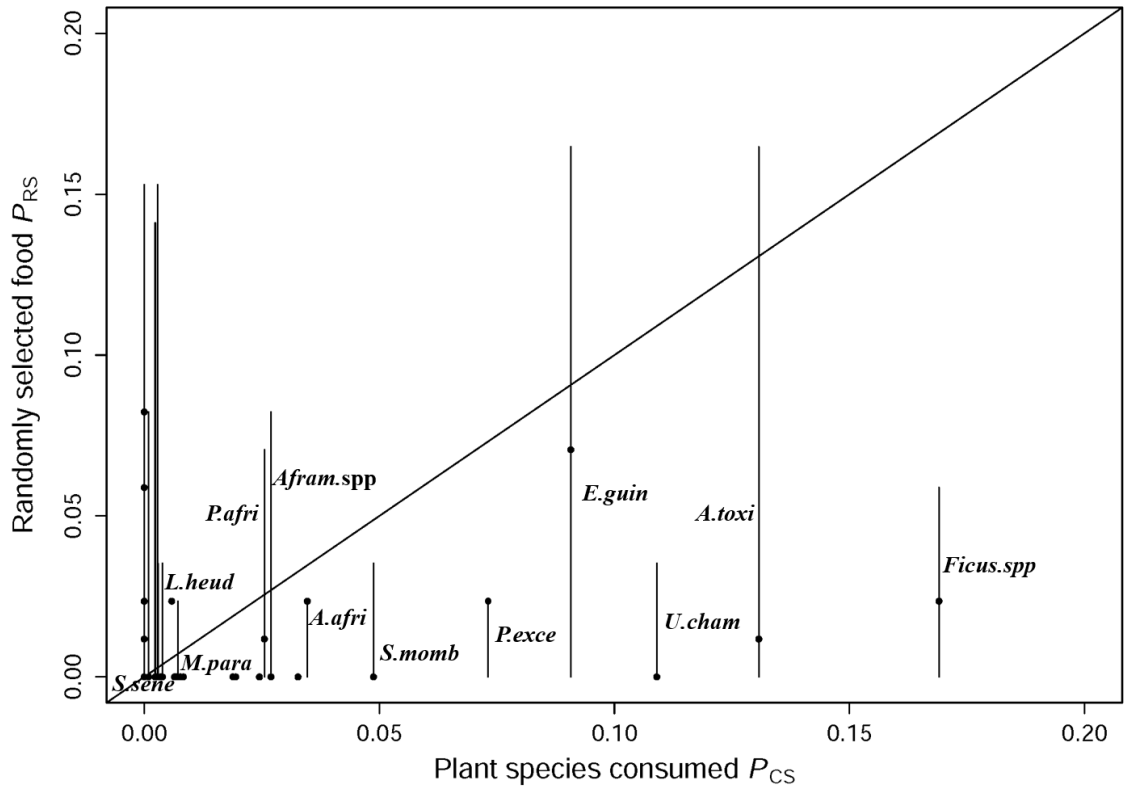

Figure 7. Expected proportions based on random sampling with replacement (1000x) of fruit species consumption if the selection by chimpanzees was random (p_{RS}), as a function of observed proportions of fruit species consumed (p_{CS}). Results for *Dialium guineense*, which was much less frequently consumed than expected based on its availability, are not shown here for better visualization of the results for the other species. See Table 1 for species abbreviations.

4.4 Discussion

Temporal variation in food availability

In LCNP, leaf flushing and flowering peaks were preceded by leaf shedding that occurred during the dry season, as described for other seasonally dry tropical forests (i.e. forests with a unimodal rainfall pattern) (van Schaik et al. 1993). Moreover, these phenological stages

peaked during the dry season, which is consistent with the insolation-limitation hypothesis, i.e. that leaf flushing and flowering occurs during the sunniest time of the year. This could be an adaptation of the plant species to minimize the attack of insects on new leaves (Aide 1992, Coley and Barone 1996), given that herbivorous insects tend to be less abundant during the dry season (Janzen 1970), and to increase pollination success and net photosynthesis (van Schaik et al. 1993). These observed patterns may also in part be explained by the water-limitation hypothesis, because in many dry tropical forests leaf shedding occurs well before water stress has developed, and leaf flushing about one month before the onset of the wet season (Frankie et al. 1974, van Schaik et al. 1993). Therefore, the biotic or abiotic conditions prevailing during a certain phenophase, or in the preceding month, mediate the phenological response of plants (Tutin and Fernandez 1993, Chapman et al. 1999).

Fruiting phenology was partially coincident with flowering phenology and fruits were abundant during the dry season, in accordance with fruiting peaks documented at forested sites with a unimodal rainfall pattern (Hockings et al. 2009) or a bimodal rainfall pattern (Anderson et al. 2005). In contrast, other forested sites characterized by patterns of rainfall either unimodal (Tutin et al. 1991, Basabose 2005) or bimodal (Chapman et al. 1999, Moscovice et al. 2007) showed fruiting peaks during the wet season, as also reported for a savannah site with a unimodal pattern of rainfall (Hernandez-Aguilar 2009). Despite this variation, our data indicate that the peak in fruit abundance at LCNP occurs when conditions for seed germination are optimal, i.e. at the onset of the rainy season (Frankie et al. 1974). Because interannual variation in fruit availability may be high (van Schaik et al. 1993, Chapman et al. 2005, Watts et al. 2012b), it is important to consider these findings as preliminary due to the short duration of this study.

Spatio-temporal variation in diet

Dry season faecal samples were dominated by fruits relative to foliage and flowers, and a total of 31 plant species representing 16 families were identified. Many of these species were also documented as being consumed by chimpanzees in other dry sites (see Table 1; McGrew et al. 1988, Duvall 2008, Bertolani and Pruetz 2011, Sousa et al. 2013). Although a similar pattern in terms of the proportional representation of different food items has also been reported in other studies from chimpanzee populations living at dry sites (Suzuki 1969, McGrew et al. 1988, Hernandez-Aguilar 2009), as well as forest-dwelling chimpanzee

populations (Sugiyama and Koman 1992, Basabose 2005, Morgan and Sanz 2006, Watts et al. 2012a), the number of plant species here reported may represent an underestimate of the true dietary diversity at LCNP because only dry season faecal samples were collected.

Contrary to our initial hypothesis, dietary richness and diversity did not significantly vary among dry season periods, but significant compositional variation was found over the course of the dry season and among habitat types. Given that chimpanzee diet varies over time and dietary richness tends to increase in long-term studies (Wrangham 1977, Nishida and Shigeo 1983, Sugiyama and Koman 1992, Morgan and Sanz 2006), more research will be necessary to complement our findings and to adequately describe the full dietary repertoire of LCNP chimpanzees, specifically by including wet season faecal samples.

Contrary to expectations, monthly dietary composition was not correlated with geographic distances, suggesting that chimpanzees fed on roughly the same set of plant species over the entire area sampled. This indicates that even though they live in a highly human-modified landscape their proximity to humans does not seem to influence patterns of preferred food consumption, a notion which is further supported by the lack of an influence of settlements or roads as proxies for the presence of cultivated areas on dietary composition. In LCNP, cultivated areas occasionally provide food supplement, but chimpanzees always included wild plant foods in their diet, as documented in other dry sites (Duvall 2008, Hockings et al. 2009, Sousa et al. 2013) or forested sites (Sabater-Pí 1979, Nishida and Shigeo 1983, Tutin and Fernandez 1985).

Fruit consumption and availability

Confirming our hypothesis, dry season faecal samples were dominated by fruit items in periods of high fruit availability (Anderson et al. 2005, Duvall 2008, Hockings et al. 2009). Similarly, during peaks of leaf flushing and flowering, foliage or flower items were the most consumed (Tutin et al. 1997, Wrangham et al. 1998, Chancellor et al. 2012). However, the latter pattern needs to be interpreted with caution. On the one hand, the peak in foliage and flower occurrence in faeces in the mid dry season (MDS) could be a consequence of low sample size, as the fewest faeces were collected in MDS. On the other hand, faecal samples from the early dry season (EDS), which in terms of sampling effort is well represented,

suggest that fruit consumption decreases over the course of EDS, a trend that probably extends into MDS.

Furthermore, dietary richness in EDS was higher than in the late dry season (LDS) but more plant species fruited in LDS when more ripe fruits were available, which suggests that dietary richness of chimpanzees varies inversely with ripe fruit availability (Tutin et al. 1997, Wrangham et al. 1998, Basabose 2002, Watts et al. 2012a). This finding indicates that LCNP chimpanzees select specific fruit species for feeding.

In line with our hypothesis, chimpanzees chose fruits disproportionally to their overall availability, and some plant species were selected over others, like in other studies (Tutin et al. 1997, Lambert and Garber 1998, Moscovice et al. 2007). *Spondias mombin* and *U. chamae* were by far more consumed than expected by chance in EDS, *A. africana* in MDS, and *Ficus* spp. and *P. excelsa* in LDS. These species have also been reported to be preferred food plant species for chimpanzee populations elsewhere (Table 2). Despite no clear pattern for habitat types, *S. mombin*, *U. chamae* and *A. africana* are widely abundant in dense-canopy forest and *Ficus* spp. and *P. excelsa* in open-canopy forest (Carvalho et al. 2014). This suggests that habitat use for feeding may change according to the spatio-temporal variation in the availability of selected plant foods (Suzuki 1969, Baldwin et al. 1982, Tutin et al. 1991, Basabose 2005). In general, forest-dwelling chimpanzee populations have smaller home ranges than populations from savannah sites due to the greater food availability in forested habitats (Baldwin et al. 1982). The forest-dwelling chimpanzees at Kahuzi (DR of Congo) were shown to have greater home ranges when fruit becomes scarce in primary forest and fig fruits are abundant in secondary forest, but as they range in close proximity to primary forests overall smaller home ranges were reported in comparison to populations from savannah sites (Basabose 2005). LCNP chimpanzees nest preferentially in dense-canopy forest during the dry season (Carvalho et al. 2013). Although home range estimation was beyond the scope of this study, such an explanation also seems likely for our study site.

Fig fruits have been listed as being important components of the diet of chimpanzees throughout their range (Table 2), providing food when other resources are scarce, similar to other primates (Terborgh 1986, Tutin et al. 1997, Lambert and Garber 1998). *Ficus polita* is one of the most abundant species in open forest at LCNP (Carvalho et al. 2014), but the majority of *Ficus* spp. occur at lower abundances in the study area. *Ficus* spp. were

selectively consumed even when other species were available, suggesting that they are not exclusively a fallback food (FBF), as also documented for a dry site (Hernandez-Aguilar 2009) as well as forested sites (Tutin et al. 1997, Morgan and Sanz 2006, Chancellor et al. 2012).

As the two liana species *L. heudelotii* and *S. senegalensis*, the oil-palm *E. guineensis*, and the crop *M. paradisiaca*, were available year-round they can be regarded as FBFs, as documented for chimpanzees elsewhere (Table 2). Likewise, oil palm fruits are eaten throughout the year in other sites (Table 2). Humle and Matsuzawa (2004) found greater consumption of oil palm items during the rainy season in Bossou (Guinea) than Yealé (Ivory Coast), whereas in Seringbara (Guinea) chimpanzees never included oil-palm in their diet. Although oil palms in Bossou occur at greater densities than in Yealé and Seringbara, differences in their use as food resource among sites were not supported by clear differences in environmental variables, suggesting that these differences are cultural. Oil-palm density at LCNP is lower than for Seringbara (0.03-0.12 individuals /km^2 (Carvalho et al. 2014) *vs* 1.0 individuals /km^2 (Humle and Matsuzawa 2004)), and LCNP chimpanzees used this species both for feeding and nesting (Carvalho et al. 2014). However, as our study covered only the dry season and Humle and Matsuzawa (2004) studied feeding patterns during the rainy season, comparisons are difficult.

Hockings and McLennan (2012) conducted a systematic review about cultivar feeding by comparing chimpanzees in savannah sites and forested sites. Despite some selectivity in the choice of crop species among sites, *M. paradisiaca* consistently was the most consumed (Table 2). Cultivated foods were harder to identify in faecal samples than in feeding remains, and as few encounters with chimpanzees occurred during the study period more data will be necessary to improve knowledge about the repertoire of cultivated foods in the diet of LCNP chimpanzees. We therefore recommend that future studies collect phenological data on cultivated species that can be compared with data from wild species.

Methodological considerations

In areas with poorly habituated ape populations, using local knowledge with regard to which plant species chimpanzees feed on is an alternative that can help to improve scientific information (Sousa et al. 2013), for instance local knowledge seems to integrate scientific

knowledge and vice versa (Ericksen et al. 2005). We also relied on local knowledge in our study when implementing the phenological surveys, and about half of the species matched with those species identified quantitatively in faecal samples. Consequently, our data on fruit availability represent underestimates. For a more reliable evaluation of the relationship between dietary richness and diversity and fruit availability we recommend the collection of pilot data, i.e. preliminary analysis of faecal samples, cross-checking of this information with that provided by locals, and subsequent monitoring of the plant species identified by these two sources of information.

On the other hand, the fact that we relied on conventional faecal analysis could also have biased the relationship between dietary richness and diversity and fruit availability. Faecal samples do not provide an accurate measure of each plant item or species eaten as some items are more easily detected than others, e.g. seeds *vs* flowers. Moreover, interspecific differences in seed size could underestimate or overestimate the real consumption of the respective species. In spite of these limitations, studies relying on faecal analysis have provided important information on the fruits eaten by primates because identification is often possible to the species level as many swallowed seeds remain intact following gut passage (Tutin and Fernandez 1993). In the case of chimpanzees, most of the fruits are swallowed unharmed (e.g. 82% in Kibale Forest (Uganda) (Lambert and Garber 1998)). However, we suggest that future studies look in more detail into the nutritional analysis of plant species eaten (e.g. fruits of *E. guineensis* (Rogers et al. 1990) or fruits of *Dialium* sp. (Tutin et al. 1991)), or apply new methodological approaches, such as phytolith analyses of faecal samples (Phillips and Lancelotti 2014) or DNA-based techniques (Kohn and Wayne 1997, Yoccoz 2012, Quéméré et al. 2013).

Supplementing faecal analysis with the analysis of feeding remains is important, as shown here, because it confirmed the consumption of cultivated species, which would have been very hard to detect in faeces. We are aware that chimpanzees also consume other non-vegetative items, such as mammals, birds, insects, reptiles, among others (Anderson et al. 1983, Nishida and Shigeo 1983, Tutin et al. 1997). Long-term data on dietary richness and diversity, collected using a variety of methods, are necessary for a better understanding of the importance of non-vegetative items in the diet of LCNP chimpanzees. Finally, data on tool-use could provide additional insights since tool-use has played an important role in

broadening chimpanzee diet (Anderson et al. 1983, Boesch and Boesch 1983, Humle and Matsuzawa 2004).

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Supporting Material

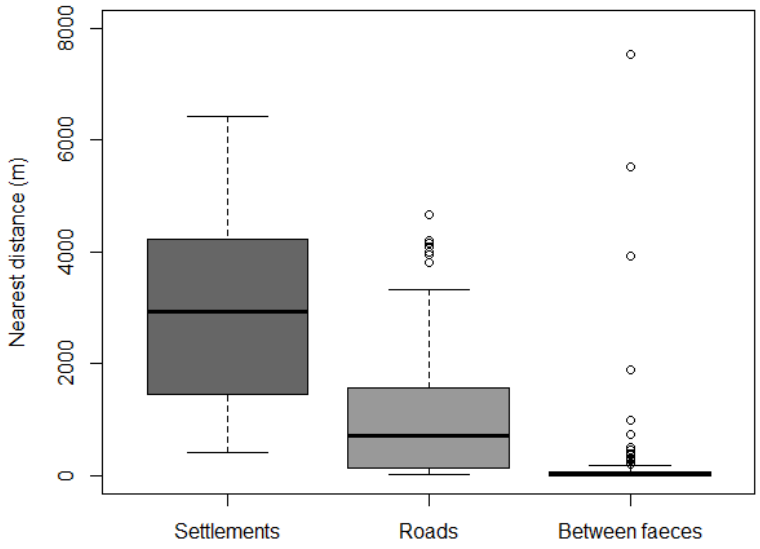

Figure S1. Nearest Euclidean distances between chimpanzee faecal samples, and between faeces and human settlements and roads, respectively. The latter can be considered good proxies for the presence of cultivated areas in LCNP.

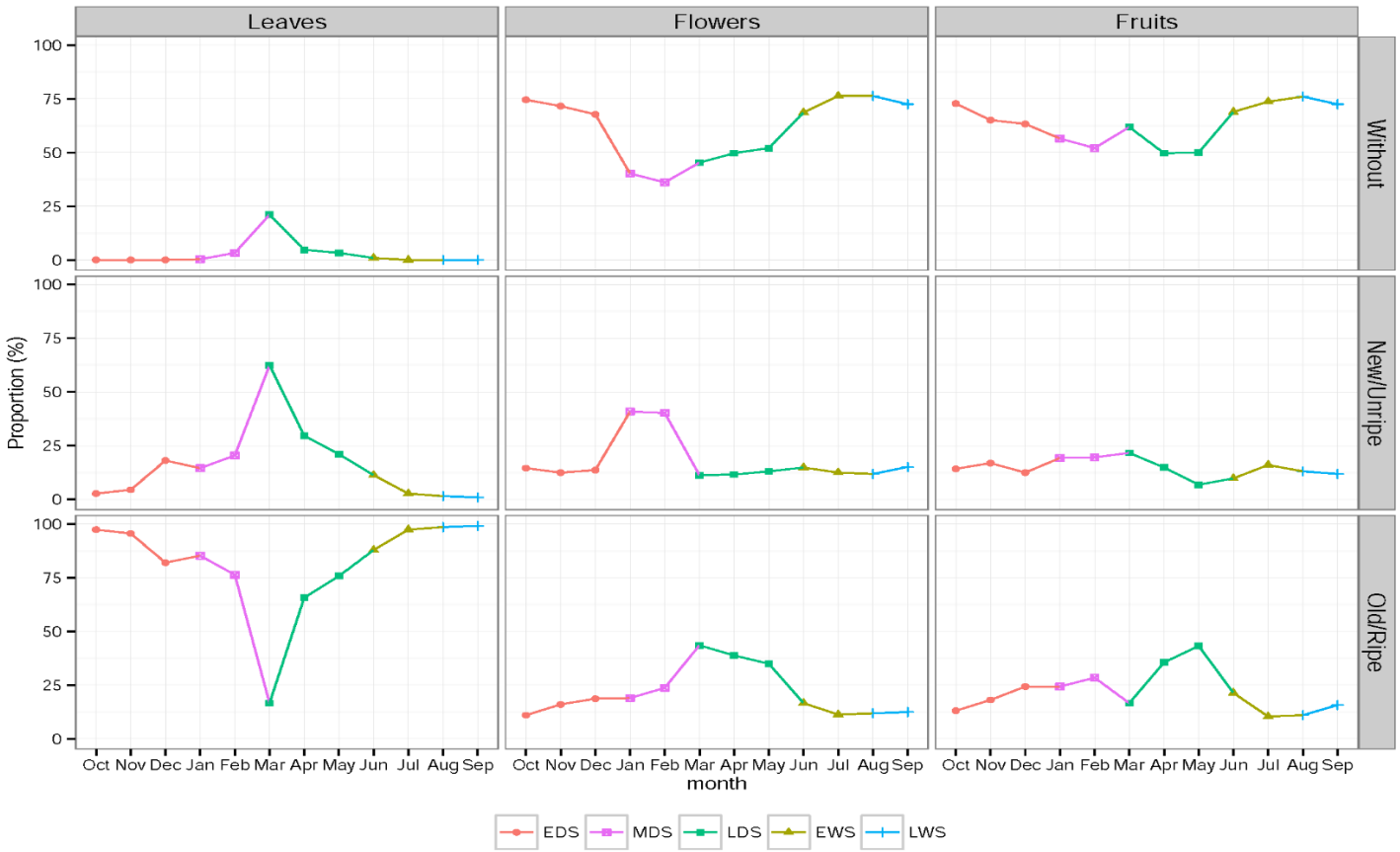

Figure S2. Proportion of phenological events recorded over 12 months in fruit trails per phenological phase. Legend: EDS - early dry season, MDS - mid dry season, LDS - late dry season, EWS - early wet season, and LWS - late wet season.

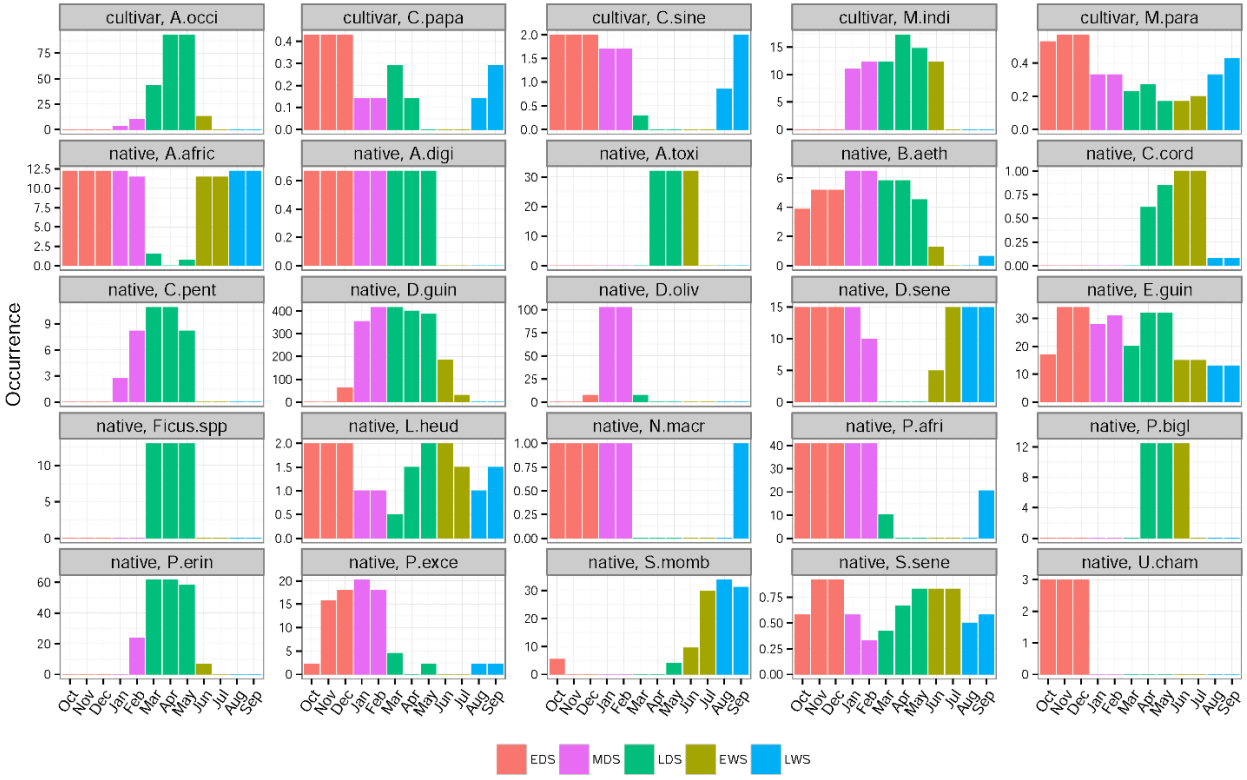

Figure S3. Monthly fruit availability index (FA_{sm}) for wild and cultivated species recorded along fruit trails. Note that the scale of the y-axis differs among species. Legend: EDS - early dry season, MDS - mid dry season, LDS - late dry season, EWS - early wet season, and LWS - late wet season. Plant species abbreviations: see Table 1.

Figure S4. Monthly plant species consumption given as % occurrence in faecal samples collected during the dry season. No data were recorded in January. Legend: EDS - early dry season, MDS - mid dry season, LDS - late dry season. Plant species abbreviations: see Table 1

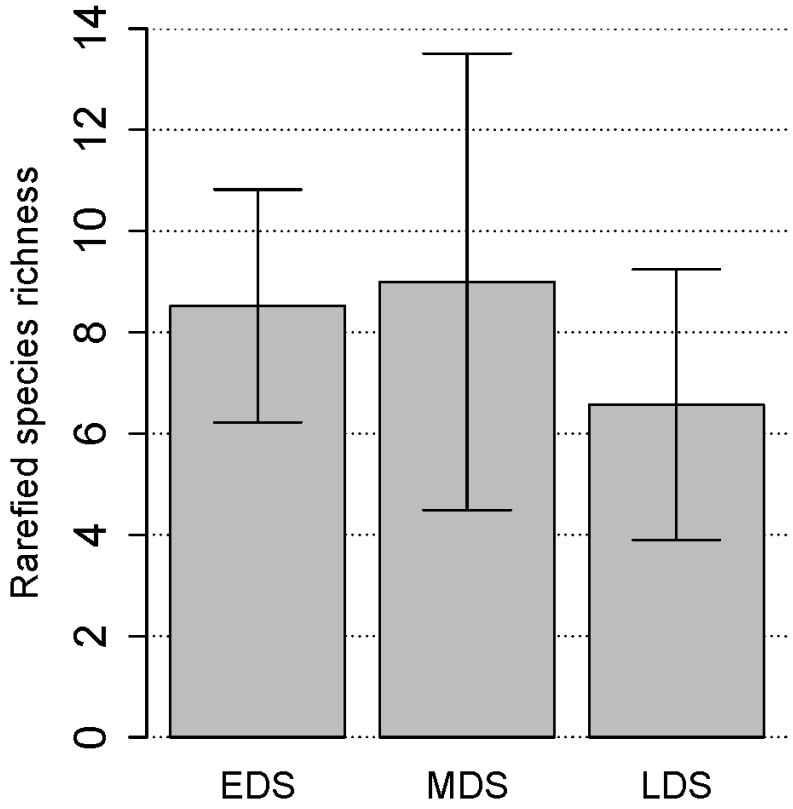

Figure S5. Temporal variation in richness of plant species consumption over the course of the dry season based on faecal analysis. Data shown are monthly means and 95% confidence intervals calculated by sample-based rarefaction analysis. EDS - early dry season, MDS - mid dry season, LDS - late dry season.

Chapter 5

General Discussion

"What we are doing to the forests of the world
is but a mirror reflection of what
we are doing to ourselves
and to one another."

- Mahatma Gandhi

5.1 General Discussion

Pan trogodytes verus has been listed as "endangered" on the IUCN Red List since 1988 (IUCN 2014), and ecological information on the subspecies at its westernmost margin of geographic distribution is scarce. This dissertation aimed to contribute to filling important knowledge gaps by evaluating population status, habitat use, nesting and feeding patterns of western chimpanzee populations in a forest-savannah mosaic landscape that is widely disturbed by humans.

The aim of this chapter is to discuss and integrate the major findings of this dissertation in the light of current knowledge about chimpanzee ecology. Further, methodological issues in the context of long-term monitoring of chimpanzee populations and the implications of this work for chimpanzee conservation are discussed. Finally, suggestions for future research are outlined.

5.1.1 Ecology of LCNP chimpanzees

As shown in *Chapter 2*, chimpanzee density estimates for LCNP were 0.50 (95% CI 0.18-1.39) and 0.22 (95% CI 0.08-0.62) nest builders per km^2 for 2010 and 2011, respectively. By comparison with previous studies published for Guinea-Bissau (Sousa 2008, Sousa 2009, Sousa et al. 2011), these estimates are the lowest yet reported for this country. Density estimates for LCNP are close to the average for other West African countries, particularly sites classified as forest-savannah mosaics (see Table S3 in Chapter 2).

Chimpanzee density estimates for LCNP varied according to habitat type. Dense-canopy forest is the least available habitat in the park, however, had the highest estimated density, contrasting with the lower density estimated for the predominant habitat, i.e. savannah-woodland. In line with other forest-savannah mosaic sites (Baldwin et al. 1981, Pruetz et al. 2008, Fleury-Brugiere and Brugiere 2010, Sousa et al. 2011), LCNP chimpanzees preferentially select dense forests for nesting during the dry season. In contrast, nest building at the easternmost limit of chimpanzee distribution (Issa, Tanzania) was mainly found in woodland during the dry season (Hernandez-Aguilar 2009). While no such evidence was observed for LCNP chimpanzees, open-

canopy forest and savannah-woodland were also used for nesting, which highlights the importance of sampling all habitat types in heterogeneous landscapes in order to obtain reliable chimpanzee density estimates. At LCNP and elsewhere, dense forest offers the most suitable habitat conditions, namely the availability of materials adequate for nesting (Koops et al. 2012), food resources (Furuichi and Hashimoto 2004) including a year-round availability of water sources (IBAP 2008), and lower incidence of human disturbance in these forests compared to other habitat types (Last and Muh 2013, Leblan 2014).

As demonstrated in *Chapter 2*, where chimpanzees build their nests is sensitive to human disturbances. Measures of human disturbance such as proximity to roads (Vanthomme et al. 2013, Fa et al. 2014) and settlements (Kuehl et al. 2009, Junker et al. 2012) have been used to predict the loss of suitable habitat for chimpanzees at small and large geographic scales. In LCNP, most roads and settlements are surrounded by agricultural areas, including extensive cashew plantations, which in turn are surrounded by open forests and savannah-woodland, restricting the occurrence of suitable trees for nesting mostly to small patches of dense forests, which are generally located farther away from human-disturbed areas. LCNP is located at the northernmost distribution limit of chimpanzee populations in Guinea-Bissau. This park is delimited by two main rivers – Corubal, in the north, and Buba, in the south – which are particularly used as transportation routes by park residents who have limited road access. Thus, rivers may have the same negative effect on chimpanzee populations as roads, i.e. facilitate the commercialization of bushmeat.

A recent study investigated the historical/social and ecological relationships between humans and chimpanzee and elephant populations by considering precolonial and early colonial (nineteenth- and twentieth-century) data from Guinea, Guinea-Bissau, and Senegal (Leblan 2014). The study suggested that chimpanzees have adapted to live alongside human populations in heterogeneous landscape modified by everyday life activities and agro-ecological management, and also that chimpanzees seldom come out into open environments, mostly foraging in the dense vegetation (Leblan 2014). Nevertheless, even though chimpanzees reportedly show a certain ability to coexist with humans (Hockings 2007, Duvall 2008, Leblan 2014), ongoing human population growth, illegal hunting, large-scale agricultural plantations, slash-and-burn agriculture,

among other factors, have been altering the extent to which sustainable land-use change has been practiced, thus compromising chimpanzee conservation efforts (Gippoliti and Dell'Omo 2003, Hockings and Humle 2003, Fa et al. 2014).

The effect of vegetation characteristics (floristic richness, diversity and composition, tree density and total basal area) on nest abundance of LCNP chimpanzees was assessed in *Chapter 3*. Higher abundance of nests was correlated with lower floristic diversity and greater availability of smaller-sized trees, both characteristics of dense forest, and may reflect its state of degradation, a scenario also reported from Bossou (Guinea) (Sugiyama and Koman 1992). Otherwise, lower abundance of nests was associated with greater floristic richness and greater variation in floristic composition, vegetation characteristics of the more open and species-rich habitats (i.e. open forest and savannah-woodland). The abundances of atelid (Cristóbal-Azkarate et al. 2005, Stevenson 2011) and cercopithecid monkeys (Rovero and Struhsaker 2007, Linder and Lawler 2012) were shown to be correlated with a similar set of vegetation characteristics explored herein, however, no comparable studies on chimpanzees are available. In Kalinzu Forest (Uganda), chimpanzee nest abundance was best predicted by fruit abundance and vegetation type, and no significant evidence was found for the effect of tree density (Furuichi and Hashimoto 2004), in line with our findings.

Restricting the analysis to important food plant species for LCNP chimpanzees, nest abundance was also related with greater availability of smaller-sized trees, congruent with a preference for nesting in dense forest. Most nests (90%) were built in feeding trees, as reported in Bwindi (Uganda) (93%) (Stanford and O'Malley 2008) and Mahale (Tanzania) (72%) (Ihobe 2005). Other studies indicate that this pattern is more prominent for day nests because night nests are not necessarily built in feeding trees, but rather in neighbouring trees (Goodall 1962, Brownlow et al. 2001). In Bwindi, no data were collected on whether nest trees had ripe fruits at the time of observation or on physical characteristics of nest trees, like in our study, and Stanford and O'Malley (2008) suggested that chimpanzees select nest trees according to tree height, maturity, height of the first branch, among other variables, and not because they are feeding trees.

In addition to assessing vegetation correlates of chimpanzee nest abundance, *Chapter 3* also explored selectivity in the choice of nest tree species. In line with other findings

from Guinea, Uganda, and Tanzania (Furuichi and Hashimoto 2004, Ndimuligo 2007, Stanford and O'Malley 2008, Koops et al. 2012), LCNP chimpanzees were selective in the choice of nest tree species, using 23 trees at different proportions, of which *Dialium guineense*, *Afzelia africana*, *Dentarium senegalense*, *Elaeis guineensis* (oil palm), *Parkia biglobosa*, and one unidentified species were selected more often than expected by chance. In contrast with findings from Cantanhez National Park (CNP), another protected area in Guinea-Bissau where *D. guineense* and *E. guineensis* were used at proportions of 2% and 92%, respectively (Sousa et al. 2011), at LCNP *D. guineense* was clearly preferred for nesting over *E. guineensis* (53% vs. 10%). However, as Sousa et al. (2011) did not record data on the densities of these tree species, comparisons are difficult. Oil-palm use for nesting has also been documented for chimpanzee populations living in Kounounkan Massif (Guinea) (Barnett et al. 1996), Bossou (Guinea) and Yealé (Ivory Coast) (Humle and Matsuzawa 2004), but not for those in Seringbara (Guinea) (Humle and Matsuzawa 2004). Humle and Matsuzawa (2004) suggested that the different use of oil-palm between Bossou, Yealé and Seringbara could not be explained by environmental differences, but may be culturally determined. Further data from a greater range of study sites, particularly on oil-palm density, are needed to better understand what determines the prevalence of oil palm use for nesting.

Patterns of nest height distribution were investigated in *Chapter 3* to evaluate evidence for or against the anti-predation hypothesis, which posits that chimpanzees at sites with predators built nests consistently higher than at those with low predation pressure. Despite no significant differences among habitat types, nest height was higher in savannah-woodland than in forested habitats, and oil palms harbored nests at greater heights and at greater diameter at breast height (dbh) than *D. guineense*. Thus, nest tree selection may be a consequence of different tree physiognomies, but without having data on physical characteristics of trees with and without nests (Pruetz et al. 2008, Hernandez-Aguilar et al. 2013), no definitive conclusion could be drawn. Arboreal nesting *per se* is evidence which supports the anti-predation hypothesis (Baldwin et al. 1981, McGrew 2004, Pruetz et al. 2008, Hernandez-Aguilar et al. 2013). The presence of leopards is reported both for LCNP (IBAP 2008) and CNP (Gippoliti and Dell'Omo 1996). However, abundance data are lacking to infer whether leopard abundance is high enough to be considered a threat for chimpanzees, as documented for Assirik (Senegal) (Baldwin et al. 1981, Tutin et al. 1983). Exclusive arboreal nesting observed at LCNP

may be a consequence of widespread human disturbance, in line with findings from Last and Muh (2013) who attributed the lack of ground nesting at one of their study sites to increased human pressure. LCNP residents reported several times that chimpanzees are hunted for bushmeat, and after killing their mothers young are sometimes captured for being traded as pets (Joana Carvalho, personal observation). Similar accounts have been documented also for the southern region of Tombali (Cá 2008). Moreover, body parts of chimpanzees are used in traditional medicine in Guinea-Bissau (Sá et al. 2012) and Alves et al. (2010) found that, among other primates, chimpanzees are used in traditional folk medicine and in magic-religious rituals.

In *Chapter 4* chimpanzee dietary richness, diversity, and composition, spatio-temporal variation in these parameters, and how they are related with food availability were explored. As documented for several chimpanzee populations elsewhere (McGrew et al. 1988, Tutin et al. 1997, Wrangham et al. 1998, Basabose 2005, Morgan and Sanz 2006, Hernandez-Aguilar 2009, Hockings et al. 2009, Watts et al. 2012), LCNP chimpanzees show an overwhelmingly fruit-based diet, composed of 31 identified plant species representing 16 families. By comparison with dietary lists from long-term studies (Wrangham 1977, Nishida and Shigeo 1983, Sugiyama and Koman 1992, Morgan and Sanz 2006), and because only dry season faecal samples were collected the number of species here reported may not represent the full dietary repertoire of LCNP chimpanzees.

Dietary composition was similar among habitat types (dense forest, open forest, savannah-woodland) and among dry season periods (early, mid, late). Also, monthly dietary composition was independent of geographic distance among faecal samples, suggesting that chimpanzees have access to and feed on roughly the same set of plant species over the entire study area. Patterns of food selection by LCNP chimpanzees do not seem to be influenced by their proximity to humans, which is further supported by the lack of an effect of proxies for the presence of agricultural areas (distances to roads and settlements) on dietary composition. It is important to note that the faecal analysis mostly led to the detection of wild species and cultivated species were rarely found. Further studies, preferably employing modern techniques such as DNA barcoding (Kohn and Wayne 1997, Quéméré et al. 2013), are needed to get a more complete and

accurate picture of the consumption of wild and cultivated species by LCNP chimpanzees.

In the early (EDS) and late dry season (LDS) chimpanzee diet was dominated by fruits, contrasting with the higher consumption of flowers and foliage in the mid dry season (MDS). In general, fruit consumption was in accordance with the increase in fruit availability over the dry season, which has also been reported from other sites characterized by either unimodal (Hockings et al. 2009) or bimodal patterns of rainfall (Anderson et al. 2005). In contrast, other sites with a unimodal rainfall pattern (Tutin et al. 1991, Basabose 2005, Hernandez-Aguilar 2009) or a bimodal rainfall pattern (Chapman et al. 1999, Moscovice et al. 2007) have fruiting peaks during the wet season. Dietary richness and diversity did not significantly vary among dry season periods. However, dietary richness was higher in EDS, when the availability of unripe fruits was higher, than in LDS, when more ripe fruits were available, suggesting that dietary richness varies inversely with ripe fruit availability, a finding in line with previous studies (Tutin et al. 1997, Wrangham et al. 1998, Basabose 2002, Watts et al. 2012).

In *Chapter 4* patterns of fruit species selectivity were also investigated. Like in other studies (Tutin et al. 1997, Lambert and Garber 1998, Moscovice et al. 2007), LCNP chimpanzees were very selective frugivores, selecting some fruit species disproportionally to their overall availability. Fruits of *Spondias mombin* and *Uvaria chamae* were commonly eaten in EDS and those of *Afzelia africana* in MDS in dense-canopy forest, while in LDS chimpanzees switched to open-canopy forest where fruits of *Ficus* spp. and *Parinari excelsa* were abundant. In LCNP, ranging patterns of chimpanzees seem to be determined by the spatio-temporal variation in the availability of selected fruit species (Suzuki 1969, Baldwin et al. 1982, Tutin et al. 1991, Basabose 2005). In general, forest-dwelling chimpanzee populations have greater food availability in forests and consequently smaller home ranges than savannah chimpanzees (Baldwin et al. 1982). Kahuzi chimpanzees (DR of Congo) increase their home range when fruit becomes scarce in primary forest and fig fruits are abundant in secondary forest, but as they occur in close proximity to primary forests, overall smaller home ranges were reported in comparison to populations from savannah sites (Basabose 2005). As shown in *Chapter 2*, LCNP chimpanzees build nests preferentially in dense forest during the

dry season. Given this evidence, LCNP chimpanzees may expand their home ranges during the dry season in response to fruit scarcity in dense forest.

Ficus spp. were selectively consumed by LCNP chimpanzees even when other species were available, suggesting that they are not exclusively a fallback food (FBF), in line with some studies (Tutin et al. 1997, Hernandez-Aguilar 2009, Chancellor et al. 2012), but not others (Wrangham et al. 1998, Marshall et al. 2009). Other species were available year-round such as *Landophia heudelotii*, *Saba senegalensis*, *Elaeis guineensis*, and *Musa paradisiaca*, and they can be regarded as FBFs, as reported elsewhere (see Table 2 in Chapter 4).

Another pattern related to plant species selection is that chimpanzees consume selected parts of certain plant species which have low nutritive value but contain bio-active compounds with anti-parasitic properties (Ohigashi et al. 1994, Huffman et al. 1996, Krief et al. 2006), including against *Plasmodium* infections (Krief et al. 2004). We recommend that future studies examine this issue.

Cultivar feeding of several chimpanzee populations was recently reviewed by Hockings and McLennan (2012), who found that chimpanzees consume up to 36 cultivated species across several study sites. Some species are also eaten by LCNP chimpanzees such as *Musa* spp. (banana), *Anacardium occidentale* (cashew), *Saccharum officinarum* (sugarcane) and *Sorghum bicolor* (sorghum). LCNP chimpanzees also consumed *Pennisetum glaucum* and *Hibiscus sabdariffa*, both cultivated species not reported in the aforementioned systematic review (Hockings and McLennan 2012). Hockings and McLennan (2012) suggested that chimpanzee populations exposed to a greater extent to agricultural areas have their diet widely composed of fruits of cultivated species rich in sugar, also showing patterns of selectivity in the choice of these species.

5.1.2 Methodological considerations

Chapter 1 provided information about appropriate sampling designs (strip transects vs. line transects) and methodologies (distance sampling, home range, nest counts) to estimate primate density and population size. What constitutes the most appropriate

design and methodology for long-term monitoring of apes remains controversial (Hashimoto 1995, Plumptre and Reynolds 1996), and substantial efforts have been made to standardize guidelines for surveys and monitoring of great ape populations (see Kühl et al. 2008). How can we reliably detect temporal trends in population size within and between protected areas? What is the best way to provide baseline information for long-term population monitoring?

As discussed in *Chapter 2,* line transect distance sampling based on randomly placed transects should be the method of choice, because it provides unbiased and robust population estimates (Buckland et al. 2001). New methodologies were developed to deal with the difficulty of detecting great apes, based on indirect signs of their evidence such as nests, dung, fingertips, or vocalizations (see Kühl et al. 2008). This study adhered to assumptions underlying nest count methods, and through application of the standing-crop nest count (SCNC) method a viable and economical way to detect chimpanzee population declines was achieved. Further, the application of the marked-nest counts (MNC) showed to be appropriate to determine the specific information on nest decay rate for LCNP as well as to assess human disturbance and define conservation measures, because nest surveys were repeated over time.

Conventional analysis of faecal samples was used in *Chapter 4* to obtain the first quantitative data on chimpanzee diet at LCNP. Despite the shortcomings of this approach, it is considered appropriate to identify and quantify the occurrence of plant items and species in faecal samples (Putman 1984, Basabose 2002, 2004, Morgan and Sanz 2006). However, robust information about the relative proportions of different consumed food items are hard to obtain using this method (Hernandez-Aguilar 2006). Moreover, as feeding remains are useful to identify cultivated species, including some species not detected in faeces, such evidence needs to be more routinely collected in future studies. For a precise species identification a combination with DNA-based techniques is also recommended and increasingly feasible (Kohn and Wayne 1997, Yoccoz 2012, Quéméré et al. 2013).

5.1.3 Conservation considerations

Most primate diversity is concentrated in poor countries characterized by political instability, where natural resources are essential for the survival of local communities. Natural resource dependence by local communities and forest conversion to extensive agricultural areas have been leading to the loss of most suitable habitats for many primates (Isabirye-Basuta 2008), even within protected areas (Plumptre et al. 2010). In the tropics, some protected areas have been effective in protecting biodiversity and ecosystems even in the context of limited funding and under growing land-use pressure, and in making a significant contribution to long-term biodiversity conservation (Bruner et al. 2001). However, many protected areas across the tropics are experiencing biodiversity loss due to the combined effects of habitat disruption, hunting, or forest-product exploitation (Laurance et al. 2012)

As we have shown, chimpanzees in LCNP are closely associated with the least available type of habitat, dense-canopy forest, which is also the one most threatened. It is urgent to implement effective conservation measures to mitigate the negative impact of extensive cashew plantations in this protected area, and consequently to conserve the remaining suitable habitat for one of the most threatened coastal chimpanzee populations. Hence, we recommend to:

- Continue the conservation measures that IBAP has been implementing in this protected area to protect and to conserve its biodiversity (IBAP 2007, 2008);
- Strengthen and enforce the hunting law of Guinea-Bissau (Decree No. 21/1980);
- Strengthen and enforce the forest law of Guinea-Bissau (Decree No. 4-A/91);
- Further consistent investment in guard training and capacity building;
- Involve park residents in co-management of LCNP and employ locals as park guards or tourist guides;
- Manage cashew plantations and other crops in areas that are already disturbed and where environmentally sustainable practices could be implemented; raise environmental awareness among temporary harvest workers during the period of cashew harvesting (March to late June);
- Promote natural forest regeneration after agricultural abandonment as a low-cost strategy to restore dense forests;

- Regulate slash-and-burn agriculture to enable colonization of seed sources from adjacent mature forests and prevent soil degradation.

In Nialama (Guinea), critical chimpanzee habitat has suffered less degradation within a Classified Forest boundary due to the benefits of co-management between local communities and government towards the sustainable utilization of these forests (Sunderland-Groves et al. 2011). Critical habitat areas for chimpanzees should be identified and quantified through long-term monitoring, both within and outside of LCNP as chimpanzees also range outside of the park boundaries (Joana Carvalho, personal observation). Recent studies have shown the importance of conserving habitat and resources outside of protected areas (Stokes et al. 2010, Jones 2011, Butsic et al. 2012). Thus, local communities need to be involved in the management of these areas to promote lower-impact land uses near the park, which will allow both them and chimpanzee populations to accrue direct benefits (Bruner et al. 2001, Sunderland-Groves et al. 2011). Moreover, it will be important to establish buffer zones around the LCNP to allow connectivity between chimpanzee populations both living inside and outside LCNP.

Some recent perspectives emerged to improve chimpanzee conservation in human-dominated landscapes such as the "indigenous conservation model" in which the agricultural environment is valued based on local community experience and knowledge (Yamakoshi and Leblan 2013). This model was implemented at Bossou (Guinea) and it showed to better prevent epidemics of zoonoses, as well as injuries and deaths from chimpanzee attacks, than conservation approaches based on general knowledge from conservation ecology. Yamakoshi and Leblan (2013) suggested that this model needs to be extended to other chimpanzee populations that live in the proximity of agricultural areas, as is the case of LCNP chimpanzees.

There is a lack of landscape-scale data to develop general action plans for primate conservation (Marsh et al. 2013, Arroyo-Rodríguez and Fahrig 2014). From an ecological point of view, a landscape is defined as a heterogeneous land area composed of a mosaic of different land cover types such as forest patches, agricultural areas, vegetation corridors and human settlements (Arroyo-Rodríguez and Fahrig 2014). A landscape-scale conservation approach for chimpanzees in Guinea-Bissau, which takes

into account their ecological requirements at larger spatial scales should be considered in future studies. Many chimpanzee populations nowadays live in human-modified landscapes, and for an effective management and conservation of this species further data including all land cover types at different spatial scales are needed for a comprehensive understanding of how chimpanzees respond to land-use change.

5.2 Future Research Directions

Despite the relevant new findings reported in this dissertation, it is important to keep in mind that much of our ecological knowledge about chimpanzees was obtained through long-term studies. Several perspectives for future research based on this thesis were already mentioned throughout this chapter. Here, a few additional suggestions for directions for future work are outline.

Since an effect of seasonality on nesting patterns has been documented for other sites (Baldwin et al. 1981, Baldwin et al. 1982, Hernandez-Aguilar 2006), in future research it will be important to determine if nesting patterns observed in this study hold over the full annual cycle by collecting data over the wet season. Seasonality also has an effect on food availability and a more extensive and systematic study will be important for a more robust assessment of the full dietary repertoire of LCNP chimpanzees as well as to better understand ranging patterns of these chimpanzee populations.

This study reports the first nest decay rate for LCNP (293.9 days, %CV=58.8), which was close to estimates documented within the subspecies' range (see Table S4 in Chapter 1). However, as this estimate applies only to the dry season, it would be important to collect data also during the wet season to determine if there are seasonal differences in nest decay rate or whether it remains stable over the full annual cycle.

Floristic richness, diversity and composition, tree size and density, and fruit abundance are commonly used predictor variables in studies assessing correlates of primate abundance (Wieczkowski 2004, Cristóbal-Azkarate et al. 2005, Rovero and Struhsaker 2007, Linder and Lawler 2012), but there are no previous studies on chimpanzees that have related nest abundance with these vegetation characteristics, making comparisons difficult and highlighting the need for future studies.

At the nest tree species scale, physical characteristics such as tree height and the height of the lowest branch seem to better explain nest height, but these data are only available for few study sites (Hernandez-Aguilar et al. 2013). Hence, we recommend collecting these data in LCNP to better understand which tree physical characteristics are most important in influencing nest tree choice. Furthermore, the selection of sleeping sites and the function of arboreal nesting should be more thoroughly investigated, and go beyond an evaluation of the anti-predation hypothesis to also assess whether patterns of nest height distribution might be explained by other strategies related to pathogen avoidance (e.g. presence of malaria mosquitoes), thermoregulation, and/or promotion of mental health.

Recent molecular techniques such as DNA metabarcoding should be considered in future studies on the diet of LCNP chimpanzees as a complementary method to conventional faecal analysis because it is a more reliable and systematic approach for studying animal diets (Yoccoz 2012).

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Appendix I. List of non-human primates described for Guinea-Bissau, including names in creole.

SPECIES	COMMON NAME	LOCAL NAME
Pan troglodytes verus	western chimpanzee	dari
Colobus polykomos	western back-and-white colobus	macaco fidalgo
Piliocolobus badius temminckii	Temminck's red colobus	macaco fatango
Papio papio	Guinea baboon	macaco kon
Cercopithecus sabaeus	Green monkey	santcho di tarrafe
Cercopithecus mona campbelli	Campbell's monkey	canculma
Cercopithecus petaurista buettikoferi	Lesser spot-nosed monkey	santcho
Erythrocebus patas	Patas monkey	santcho fula
Cercocebus atys atys	Sooty mangabey	santcho
Galago senegalensis	Senegal bushbaby	santcho

Appendix II. List of plant species mentioned throughout the dissertation, including names in creole.

PLANT SPECIES	FAMILY	CREOLE NAME
Wild Species		
Adansonia digitata	Bombacaceae	cabaceira
Acacia macrostachya	Leguminosae / Mimosoideae	pó-de-ferida
Afzelia africana	Leguminosae / Caesalpinioideae	pó-di-conta
Albizia dinklagei	Leguminosae / Mimosoideae	faroba-di-mato
Albizia zygia	Leguminosae / Mimosoideae	pó-di-raio
Allophylus africanus	Sapindaceae	n.a.
Anthostema senegalense	Euphorbiaceae	pó-di-binhal
Antiaris toxicaria	Moraceae	pó-di-bicho
Antidesma membranaceum	Euphorbiaceae	n.a.
Borassus aethiopium	Palmae	cibe
Cassia sieberiana	Leguminosae / Caesalpinioideae	canafistra
Ceiba pentandra	Bombacaceae	poilão
Cola cordifolia	Sterculiaceae	manjandja
Combretum collinum	Combretaceae	n.a.
Combretum micranthum	Combretaceae	chá-de-buco
Combretum nigricans	Combretaceae	pau-de-pilão
Cremaspora triflora	Rubiaceae	n.a.
Crossopteryx febrifuga	Rubiaceae	n.a.
Crotalaria hyssopifolia	Leguminosae / Papilionoideae	n.a.
Dalbergia boehmii	Leguminosae / Papilionoideae	n.a.
Daniellia oliveri	Leguminosae / Caesalpinioideae	pó-di-incenso
Detarium senegalense	Leguminosae / Caesalpinioideae	mambode
Dialium guineense	Leguminosae / Caesalpinioideae	veludo
Dichrostachys cinerea	Leguminosae / Mimosoideae	pó-di-ferida-preto
Diospyros heudelotii	Ebenaceae	n.a.
Elaeis guineensis	Palmae	palmeira-de-óleo
Erythrina senegalensis	Leguminosae / Papilionoideae	po-di-osso
Erythrophleum guineense/ E. suaveolens	Leguminosae / Caesalpinioideae	manconi
Euphorbia schimperiana	Euphorbiaceae	n.a.
Ficus glumosa	Moraceae	Pau-de-leite
Ficus lutea	Moraceae	n.a.
Ficus natalensis	Moraceae	n.a.
Ficus polita	Moraceae	figueirinha
Ficus sur	Moraceae	n.a.
Funtumia africana	Apocynaceae	n.a.
Hexalobus monopetalus	Annonaceae	Mambumba
Khaya senegalensis	Meliacease	Bissilão
Landolphia heudelotii	Apocynaceae	fole-pequeno

Landolphia owariensi/Saba senegalensis	Apocynaceae	fole-de-elefante
Lannea acida	Amaranthaceae	pó-di-saia
Lophira lanceolata	Ochnaceae	Mené
Malacantha alnifolia	Sapotaceae	Lixa
Mezoneuron benthamianum	Leguminosae / Caesalpinioideae	unha-di-onça
Mitragyna inermis	Rubiaceae	pau-de-motom
Morinda geminata	Rubiaceae	bulungu-djubá
Neocarya macrophylla	Chrysobalanaceae	tambacumba
Newbouldia laevis	Bignoniaceae	manduco-de-feticero
Oxythenanthera abyssinica	Dioscoreaceae	cana-bambu
Parinari excelsa	Chrysobalanaceae	mampatace
Parkia biglobosa	Leguminosae / Mimosoideae	faroba
Paullinia pinnata	Sapindaceae	cinco-folha
Pericopsis laxiflora	Leguminosae / Papilionoideae	n.a.
Piliostigma thonningii	Leguminosae / Caesalpinioideae	pó-di-kankora
Prosopis africana	Leguminosae / Mimosoideae	pó-carvão
Pterocarpus erinaceus	Leguminosae / Papilionoideae	pó-di-sangue
Ricinus communis	Euphorbiaceae	djague-djague
Sarcocephalus latifolius	Rubiaceae	tambacumba-de-santcho
Spathodea campanulata	Bignoniaceae	n.a.
Spondias mombin	Anacardiaceae	mandiple
Strophanthus hispidus	Apocynaceae	malila-de-cabelo
Terminalia albida	Chrysobalanaceae	culeme
Terminalia macroptera	Combretaceae	macite
Uapaca togoensis	Euphorbiaceae	n.a.
Uvaria chamae	Annonaceae	banana-santcho
Voacanga africana	Apocynaceae	pau-de-borracho
Xylopia aethiopica	Annonaceae	malagueta-di-mato
Cultivated Species		
Anacardium occidentale	Anacardiaceae	cadjú
Carica papaya	Caricaceae	papaia
Citrus sinensis	Rutaceae	larandja
Hibiscus sabdariffa	Malvaceae	baguitche
Mangifera indica	Anacardiaceae	mango
Musa paradisiaca	Musaceae	banana
Pennisetum glaucum	Gramineae	midjo-preto
Saccharum officinarum	Gramineae	cana-de-açucar
Sorghum bicolor	Gramineae	midjo-cabalo

n.a.- not available.

Acronyms and abbreviations

AIC	Akaike's Information Criterion
AICc	Corrected Akaike's Information Criterion
BA	Total basal area
BNP	Boé National Park
CCA	Canonical correspondence analysis
CNP	Cantanhez National Park
DBH	Diameter at breast height
DF	Dense-canopy forest
e^H	Exponential form of Shannon's entropy index
EDS	Early dry season
EWS	Early wet season
FAO	Food and Agriculture Foundation
FBF	Fallback food
FR	Floristic richness
GLMM	Generalized linear mixed effects model
IBAP	Instituto da Biodiversidade e das Áreas Protegidas
IUCN	International Union for Conservation of Nature
LCNP	Lagoas de Cufada Natural Park
LDS	Late dry season
LWS	Late wet season
MDS	Mid dry season
MNC	Marked nest counts
NMDS	Non-metric multidimensional scaling
OF	Open-canopy forest
PNLC	Parque Natural das Lagoas de Cufada
SAV	Savannah-woodland
SCNC	Standing crop nest counts
SU	Sampling units
ZANB	Zero-altered negative binomial
ZAP	Zero-altered Poisson
ZINB	Zero-inflated negative binomial
ZIP	Zero-inflated Poisson